MECHANISMS OF MULTISENSORY INTEGRATION AND ATTENTION

NUNO MIGUEL MATIAS GAMA MOTA, MSc

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ABSTRACT

Spatial attention is an essential mechanism that helps us perceive our surroundings by bringing into consciousness environmental occurrences or objects that may be of importance. Studies of spatial attention have classically recorded behavioural responses to targets presented in a region of space where attention had previously been allocated to. Such investigations show a behavioural facilitation at the same location due to cueing, but less in known about the effects of shifts of attention when the cued location is not the location of interest. This thesis presents seven experiments aimed at investigating this by implementing and revising the attentional repulsion effect (ARE). The ARE is a perceptual localisation error when attention is diverted from the region of interest and it has been extensively studied in the visual domain, however, the rising number of ARE studies has created numerous research methodologies used to evoke the effect, which may have led to isolated reports. This thesis attempts to combine past methodologies with a new approach to quantify the effect, and will address some methodological differences evident in the literature, in order to optimise the stimulus paradigms and maximise the effect. The results show that a robust ARE can be elicited in the visual modality, but the same is not observed in the auditory modality. Furthermore, when using cues that are of different modality than the targets, the ARE is only observed in the visual target modality. Using visual cues and auditory targets will produce an attraction effect, in line with the ventriloquism theory. However, the implementation of interstimuli intervals up to 1.5 seconds would be enough to disrupt the ventriloquism illusion, but it did not alter the resulted attraction. Lastly, one question regarding the role of attention in sensory adaptation was

addressed. I hypothesise that sensory adaptation could be further a contributor to the ARE given that most psychophysics paradigms of the ARE repeat the same stimuli thousands of times, uninterruptedly. The results are inconclusive mainly due to experimental design. All results are discussed in relation with theories of spatial and multimodal attention.

ACKNOWLEDGEMENTS

I would like to thank the Medical Research Council, UK, for the grant without which this thesis could not have been produced. Many thanks to the IHR (Institute of Hearing Research, Notts) for having me during my PhD studies. I would also like to thank my supervisors Prof. Alan Palmer, but particularly Dr Ian Wiggins for their support. To Dr. Christian Füllgrabe for the talks (that were never that long) and for being my dearest friend. To Dr. Katrin Krumbholz for her guidance and to Vicky for tolerating my bad jokes in the office.

But now, the really important bit:

To Chloe and to Jasmine, without whom none of this would have ever been possible, and to my best friend and life partner Inês, who always candidly and tirelessly believed in me. I sincerely hope you are a daily presence in my life.

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LIST OF ABBREVIATIONS

AA – auditory cue and auditory target

AAE – attentional attraction effect

AC – auditory cortex

AIA – (auditory) attention in adaptation

ANOVA – analysis of variance

ARCMIN – minutes of arc

ARE – attentional repulsion effect

AV – auditory cue and visual target

BBN – broadband noise

BOA – behavioural observation audiometry

CN – cochlear nucleus

CTOA – cue-target onset asynchrony

EE – contralateral excitatory, ipsilateral excitatory

EEG – electroencephalography

ES – effect size

GOF – goodness of fit

IC – inferior colliculus

IE – contralateral inhibitory, ipsilateral excitatory

ILD – interaural level difference

IOR – inhibition of return

ISI – interstimulus interval

ITD – interaural temporal difference

LGN – lateral geniculate nucleus

LSO – lateral superior olive

MEG – magnetoencephalography

MGB – medial geniculate body

MSO – medial superior olive

NLRM – nonlinear regression model

PET – positron emission tomography

PSE – point of subjective equality

PTA – pure tone audiometry

RF – receptive fields

RT – reaction/response time

S:N – signal to noise ratio

SC – superior colliculus

SOA – stimulus onset asynchrony

SOC – superior olivary complex

VA – visual cue and auditory target

VAIA – (visual) attention in adaptation

VRF – visual receptive field

VV – visual cue and visual target

ABOUT ME

I completed my first undergraduate degree in Sports Science at the Technical University of Lisbon, Portugal. Alongside this course, I was also studying in a Jazz degree at night. The sports science degree was extremely interesting because it combined disciplines such as biochemistry and anatomy but it left out my interest for music. Thus, after becoming a qualified PE teacher, I decided to travel to the UK for a second "first" degree in Audio and Music Technology. Soon I had developed an interest for the neuroscience of sound, and the completion of this BSc with a First Class Honours and a "Best Dissertation Award" (on capturing analogue sound sources) encouraged me to attempt more academic pursuits. I completed an MSc in Clinical Audiology at The University of Manchester, and during that time I worked with the Manchester Cochlear Implant (CI) research team, led by Professor Colette McKay. My MSc dissertation focused on automated cochlear implant fitting, using EEG techniques. In particular, I was interested in using EABRs (an electric form of auditory brainstem responses) to assess cochlear nerve survival. I very much enjoyed working with CI patients and the casual chats about how they perceive sounds in general were puzzling and very appealing to me.

I was very motivated to pursue a PhD and a career in cochlear implant research, thus I applied to the University of Nottingham for a Doctoral project in basic research of plasticity in cochlear implantees, funded by the Medical Research Council. I was successfully awarded a full MRC studentship to work on the project, which proposed to measure the prevalence of unimodal auditory and visual and bimodal cells in the centre of A1 (the primary auditory cortex), and to study them after deafness had been induced. The last stage of the research project was the most important and appealing to me, as deaf animals would be implanted with a cochlear implant and exposed to sounds, to ascertain to which extent the cochlear

implant could revert the plastic changes that occurred during deafness. Implanting animals with CIs is a very challenging and sought surgical skill and was the reason I chose this PhD project out of two other I had applied to (music or speech perception with CIs). Unfortunately this initial project was abandoned and the PhD shifted focus, but the data collected during my first year can be found in Appendix C.1.

During my PhD I was awarded a fellowship with the Auditory Cognitive Neuroscience Network (ACN) and visited[1] the international laboratory for Brain, Music, and Sound Research (BRAMS), in Montreal, Canada, for nine months. During that time I published a commentary entitled "Compensatory plasticity, time matters." an insight on the importance of age at (cochlear) implantation, and I have led and completed two other studies on speech and auditory brainstem responses (one of them submitted to publication and the other currently being written).

Before moving on to chapter one, I would like to explain that of each chapter of this thesis is marked by a single page of numbers (a chapter cover, if you like). Given that the overarching topic of the thesis is visual attention, this visual search game marks the beginning of each chapter. For the past weeks I have been playing this association and a visual search game that with my (3 year old) daughters. I tell them there are two aims: one, to count how many black numbers there are, to create an association between the shape of the number and quantity; the second is to find where the sole grey number is (that is the same as the black ones). Black numbers are the corresponding number to the chapter. Thus, for chapter two, one has to count two number 2 and find a third grey one hidden in the midst of all the other random grey numbers.

[1] My doctoral studies were interrupted for this purpose and I was sponsored by an ERASMUS MUNDUS studentship.

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CHAPTER 1 THESIS INTRODUCTION

This thesis is concerned with spatial attention. It presents empirical evidence collected through a series of experiments that aimed to explore the role that attention orienting to irrelevant locations will have on the spatial perception of foveated space.

In this chapter, I start by explaining the focus of the thesis and explain the reasons for researching spatial attention using the attentional repulsion effect (ARE) as a theoretical framework. Then I present the broader context of attention related studies. Finally, I outline the structure of the thesis.

1.1. FOCUS OF THE THESIS

Three years ago, our twin daughters were born. Since then, I have become aware of how (in the past) I undervalued the importance of "attention" in daily life. This personal realisation arose from countless repetitions of (probably) the most spoken words by parents of toddlers: "Pay attention, please…". Whether at the dinner table, the park, crossing the street or playing at the beach, paying attention to surroundings is perhaps the most fundamental of survival mechanisms[2]. Since the birth of our twins, attention to my (and their) surroundings has taken a different perspective. Similarly, extrapersonal space has also taken a new dimension and attention demands are greater than ever to assure I can separate harmless occurrences from those that are truly damaging. As for the twins, they are learning how

[2] This is also a personal realisation from speculating on the outcomes of not paying attention to the coming, respectable sized wave, while playing in the sand with backs turned to the ocean.

to attend to crucial events (such as a car coming), and at the age of three, they are beginning to understand and predict outcomes.

While our world is notably multisensory and selecting between a swarm of sensory occurrences is a constant and demanding task, attentional and multisensory events have traditionally been studied in isolation. However, natural events do not typically occur in sensory isolation (in one modality only): the smell of food is accompanied by its sight and taste, whereas the sound of the wind is complemented by the proprioception of the skin and/or by the sight of a moving tree. Although it is important to understand the basic mechanisms of each cognitive process associated with each sensory modality, the transfer to reality is greater when studying these events in combination. In this thesis, we will study both unimodal and crossmodal (auditory and visual) attentional effects.

Attentional studies using a cue-target paradigm have mostly shown a facilitatory effect at the attended (cue) side. Capture of attention by abrupt visual onsets were first introduced by Eriksen and colleagues in the early seventies (Eriksen and Rohrbaugh 1970b; Eriksen and Hoffman 1972, 1973) using a cue leading paradigm. The classical zoom lens model of attention deployment was the first to successfully integrate extrapersonal spatial awareness into the apparent effects of attention (increased accuracy and faster reaction time). The reader is directed to Eriksen and James (1986), the last of a series of studies around this model. Very succinctly, in this paper, the authors propose that attention to space is very much like a zoom lens, with more detail when zoomed in, but with less spatial coverage. But, these studies were commonly performed under conditions of unimodal visual stimulation and were mostly aimed at investigating the facilitatory effect of

attention in reaction time (RT). Misrepresentation of extrapersonal space brought upon by shifts of attention towards an unexpected transient, arrived later (Suzuki and Cavanagh 1997) and have confirmed that if attention facilitates perceptual processing at the attended location, then, this comes at a cost at unattended space. The importance of this finding can be related to several daily life situations where arguably the most significant one can be found in motoring. It is not uncommon today to have countless distractions when driving a car. The sides of the roads are bursting with billboards and adverts, most of which using flashing lights and contrasting colours. The purpose of these adverts is clear: to draw the attention of the motorist. Attention can be reflexively pulled away from the location of interest, the road in front. For example, a motorcycle filtering through the traffic will have its mirrors (or indicators) passing inches away from the side mirrors of cued traffic. Spatial miscalculations in the front, brought upon by sideward distractions, can theoretically be the cause of road accidents, which can be avoided by, for example, studying fundamental phenomena like the ARE, and later transfer this knowledge to real life situations.

The ARE paradigm shows for the first time influences of a peripheral distractor (that draws attention to itself) on the spatial perception of another visual object (the object of interest) that is placed in a different location (where fixation is on-going). In the past, the ARE was conducted in conditions of unimodal visual and crossmodal visual leading, but not unimodal auditory, nor crossmodal auditory leading conditions. In this thesis we test the ARE phenomenon under all unimodal and crossmodal combinations of visual and auditory conditions, and observe that mislocalisation errors come in form of

repulsion of targets away from cues, as it is the case for the majority of ARE studies, but, we have found attraction effects that are brought upon by manipulating the cue and targets' leading or following positions and their interstimulus interval (ISI). The literature review can be found in the next chapter (2) and, following it, the General methods chapter (3).

The aim of this thesis is to investigate how the spatial perception of normal hearing and normal vision individuals is shaped by peripheral cues that exogenously pull attention away from the location of interest (the foveated location). The overarching research questions were aimed at establishing the ARE in all combinations of unimodal and crossmodal conditions of visual and auditory stimulations. More specifically, I ask if the ARE is a visual alone phenomenon or if it is possible to be observed in an audio-visual crossmodal event and in a unimodal auditory event. Furthermore, since the paradigm used to elicit this phenomenon can arguably induce a state of sensory adaptation, this thesis also aims to investigate how attending to an adapter shapes the spatial perception of a target in a ARE-like paradigm.

1.2. BROADER CONTEXT

The specific focus of this thesis is on the attentional repulsion effect. Attention is studied in a variety of disciplines, such as visual search (Wolfe 1994) or speech perception (Bronkhorst 2000), and have been shown to influence memory (Robinson 1995), pain (Eccleston and Crombez 1999), object recognition (Rutishauser et al. 2004), or even music performance (Bigand et al. 2000), to name but a few. Though attention may be considered an overarching mechanism that ultimately

shapes cognition and operates at all levels (from single cells, Moran and Desimone 1985; to perception, Posner and Petersen 1989), each discipline has its very own niche. Due to the breadth of research, a comprehensive review of attention across disciplines is an extremely ambicious and certainly beyond the scope of this thesis. Thus, the next chapter (chapter two) will focus on attention in space and will review the fundamental concepts of spatial attention orienting. However, a fundamental definition as well as a brief history of attention will be provided to Furthermore, it will present a more in depth in review of the attention repulsion effect (ARE)[3]. The ARE is a mislocalisation of space when attention is diverted away from the locus of interest. In other words, when judging a centrally positioned visual target, errors in localising it will occur when a cue is flashed at the sides. In the original study (Suzuki and Cavanagh 1997) the perception of the targets were found to be repulsed away from the cues.

1.3. STRUCTURE OF THE THESIS

This thesis consists of eight chapters. Chapter two contains a review of the literature relating to the coding of space, and attention (attention and memory, attention to space, and mislocalising space).

Chapter three, the general methods chapter, presents information about materials, experimental set-up, stimuli, data analysis, and general methodology.

Chapter four comprises two experiments aimed at investigating visual influences on auditory targets. This chapter studies the ARE in its crossmodal form, with visual stimuli leading sound (visio-auditory

[3] The paradigm behind the ARE has been extensively adapted in this thesis to study crossmodal (auditory and visual) and unimodal spatial perception.

ARE). This is the first time the ARE is investigated in a paradigm where leading cues are visual and following targets are auditory (VA). A different form of crossmodal ARE has been proposed in the past by Arnott and Goodale (2006), albeit with auditory cues and visual targets (AV).

This form of audio-visual (AV) ARE is the focus of Chapter five, which will suggest a different paradigm to study this phenomenon.

Chapter six will revisit the original ARE in its unimodal visual form (VV; in a first experiment), and will investigate if this effect is also found in the auditory domain (AA; in a second experiment).

Presently, it is unknown if it is attention that solely underlies the ARE, or if adaptation also plays a role in such spatial mislocalisations; thus, Chapter seven will investigate the fundamental relationship between spatial attention and adaptation in an ARE-like task.

Chapters four to seven present experimental work and follow the same structure. This structure consists of a short introduction that presents the rationale and key literature for the experiment(s) presented in the chapter; this is followed by the methods (participants, materials, stimuli, procedure) and the results specific to the experiment(s) presented in each chapter. Similarly, these chapters present short discussions that examine methodological and theoretical aspects relevant specifically to what is presented in the chapter. These "interim" discussions will then be developed in the general discussion (chapter eight).

Chapter eights will contain the general discussion of this thesis, which will contain an in depth discussion of the findings and will suggest

several research questions for future research, raised from the results from the chapters herein.

At the end of the thesis the reader can find the appendices, which will adopt the same number convention as the relating chapter. So, for instance, Appendix C.4 contains the appended pages of Chapter 4. An exception is made to Appendix 1. In this particular appendix (1) the reader will find the "in vivo" neurophysiological experiments aimed at investigating neural plasticity following cochlear implantation. These experiments were the original intent of my PhD and aimed to use an animal model to study plasticity under deafness, and after hearing had been reinstated with a cochlear implant device. This project was discarded but the investigations therein are still relevant in the context of multisensory integration, and will be recalled in this thesis whenever relevant.

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CHAPTER 2 LITERATURE REVIEW

2.1. INTRODUCTION

Many studies have reported on the effects of attending to a location in space. Although this review will cover attentional concepts such as covert and overt and endogenous and exogenous, and even though it will also cover the costs and benefits of attending to a region of space, the bulk of this review will focus on the attentional repulsion effect (ARE), a phenomenon that helps us understand the outcome of shifting attention outside the region of interest. In the start of this review (section 2.2, the coding of space) I will present the fundamental aspects of spatial encoding by the visual and auditory systems, and will give evidence for the superior role of vision in spatial perception.

2.2. THE CODING OF SPACE

This section will discuss how each system (auditory and visual) determines the location of an object in its modality (a sound or a light). This purpose requires the review of the fundamental organisation of each sensory system, however, I will bypass the transduction mechanisms of converting sound (in the cochlea) and light (in the retina) into the electrical potentials that travel the auditory or optic nerve. Because all experiments in this thesis will in some form investigate the spatial performance of both auditory and visual modalities, it is important to establish each modality's proficiency in representing space. This is done in the last subheading of the present section (2.4.3), where I will discuss and present evidence for the superior role of the visual sensory system in spatial encoding.

2.2.1. **The coding of light**

When light reaches the eye, the transduction of the physical energy to electrical impulses is taken cared by the retina's photoreceptors. There are two main types of photoreceptors in the retina, the cones and the rods (figure 2-1), and both present anatomical and functional specific characteristics (Young and Droz 1968; Young 1971a, 1971b; but see Tovée 2008; or Westheimer 2008).

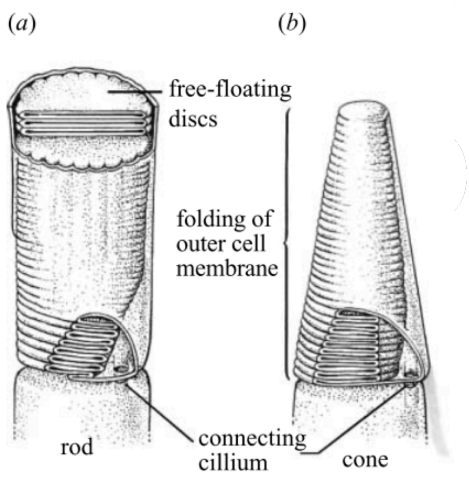

Figure 2-1 Schematic of the mammalian rod (a) and cone (b), showing the histological differences in the outer segments that contain the photopigment molecules. Adapted from Westheimer (2008).

The outer segments of the rods are cylindrical in shape and contain a much larger quantity of discs (a membranous folding that float freely in the case of the rods) where the photopigment lives (e.g rhodopsin). The most remarkable difference between rods and cones is functional, derived from histological differences related to the type of photopigment embedded in the discs. While rods are exclusively populated by rhodopsin, making them achromatic, the cones have three types of opsins and can be subdivided into three types of cells, each one with a different spectral position of their preferred frequency: S-, M- and L-cones, with reference to short, medium and long wavelength sensitivity (Stockman and Sharpe 2000). Response comparisons

between the three types of cones is what enables tricoloured vision in humans. The higher number of photopigments in the rods makes them much more sensitive to light than cones, reason why at low-light situations, vision will mainly rely on rods for. The distribution of rods and cones in the retina varies, as indicated in figure 2-1. Cones are present in low density scattered throughout the retina, with a sharp increase in density in the fovea. This is accompanied by a sharp decline in the density of rods. The fovea is exclusively populated by cones, in a one-to-one relationship with the ganglion cells. Rods, on the other hand are present in high density across the retina. This representation

Cortical magnification (Daniel and Whitteridge 1961; Cowey and Rolls 1974; Levi et al. 1985)

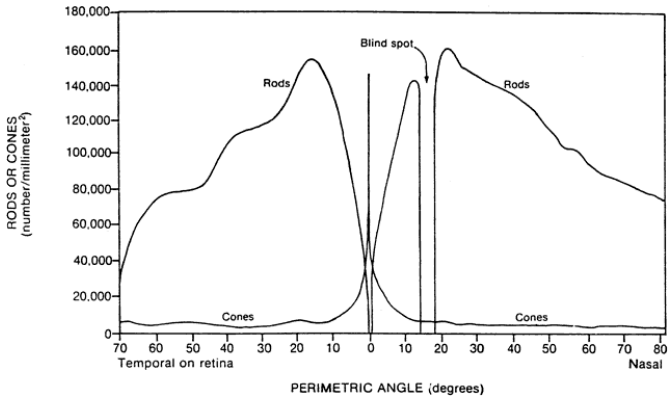

Figure 2-2 Distribution of rods and cones in the retina. Cone density is greatest at the fovea, rapidly declining with eccentricity. Adapted from Osterberg (1935)

Visual information in the mammalian nervous system is processed sequentially as it travels along the ascending pathway, and neurons along this pathway exhibit different receptive field (RF) configurations (DeAngelis et al. 1995). The RFs of ganglion cells in both mammalian (Kuffler 1953) and non-mammalian (Barlow 1953) retinas, as well as bipolar cells (Dacey et al. 2000) show a "centre-surround" response pattern. As can bee seen in figure 2-3, the centre-surround pattern is

characterised by two circles: a smaller one in the centre and a broader one in the periphery.

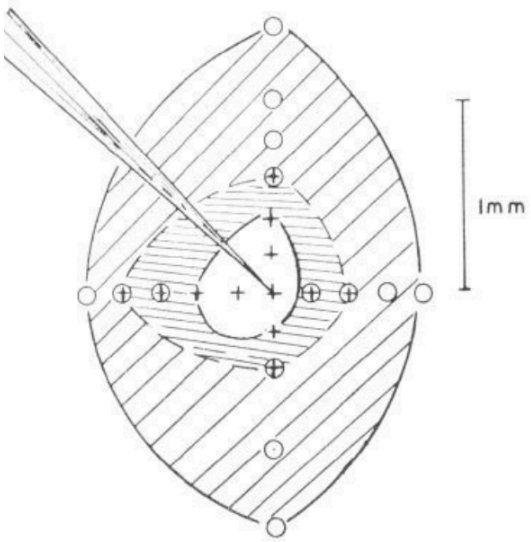

Figure 2-3 Centre-surround RFs pattern of a ganglion cell. Adapted from (Kuffler 1953). In this schematic, the tip of the electrode is shown. On responses were found in the centre of the RF (crosses) and "off" discharges were found in the peripheral regions (empty circles).

The RFs of the ganglion retinal cells are influenced by the type of bipolar cells that precede them. Bipolar cells can be divided into two groups, ON or OFF cells. ON cells depolarise in reaction to light and OFF cells are hyperpolarised by light (Kuffler 1953; Croner and Kaplan 1995; Dacey et al. 2000). RFs become more complex as we ascend in the visual stream. For example, ganglion cells also exhibit the centre--surround architecture of their RF, however, instead of depolarising or hyperpolarising, the ganglion cells will increase or decrease their firing rate. LGN neurons also exhibit this approximately circular RF organisation (Kuffler 1953; Hubel and Wiesel 1962), but, in the striate cortex, spots of light (that Kuffler had found effective in ganglion cells) may not be the most effective stimuli to activate neurons, as observed by Hubel and Wiesel in their initial findings in 1959 (Hubel and Wiesel 1959). The "pointillism" of the retina was shown to be transformed to a more complex RF in the striate cortex and in their second paper, Hubel

and Wiesel (1962) referred to two types of neurons (the simple and complex cells), but the complex cell's "*strict requirements for shape and orientation of the stimulus were in marked contrast to the relatively large leeway of the stimulus in its ordinate position on the retina*" (Hubel and Wiesel 1962, p115). RFs in the striate cortex is no longer concentric and cells exhibit a higher selectivity for visual stimulation, being more effective with motion (particularly for complex cells), orientation and directions.

2.2.2. **Visual space**

The region of space we can see without moving our eyes or head is called the visual field. In humans, each eye can only see a portion of this visual field. It is possible to divide the total field of view into two visual hemifields: the right visual hemifield is coded by neurons placed in the nasal portion of the right retina and the temporal portion of the left retina, while the left visual hemifield is coded by neurons in the nasal portion of the left retina and in the temporal portion of the right retina[4]. This forms the first stage of the sensory transduction process in the retina (by rods and cones), the visual system allocates regions of space to particular neurons. When discussing visual fields it is important to note that sight from both eyes overlap extensively in the central portion of the total field of view, which is the region of binocular field of view. The peripheral region is entirely monocular, coded by the nasal portion of the retinas. If we follow the signal from the retina into the brain, the first important stage to understand spatial perception is the optic chiasm, a junction where the nerves from the two eyes are joined together. Here, axons from the ganglion cells of the nasal portion of the

[4] Whenever not cited, the information regarding the fundamental anatomy and organization of the visual system can be found in textbooks of the specialty. The author used Tovée (2008) and Brazis (2011) as support materials.

retinas crossover to the opposite side of the brain, while axons from the ganglion cells from the temporal portion of the retinas project to their own side of the brain. Thus, each brain hemisphere receives information from the opposite visual field. The majority of these axons terminate in the first thalamic nucleus of the visual pathway, the lateral geniculate nucleus (LGN), although they also project to other nuclei (the superior colliculus, the suprachiasmatic nucleus and the pretectum). The right LGN receives information from the left visual field (coded by the nasal left retina and temporal right retina), while the left LGN receives information from the right visual field (coded by the nasal right retina and temporal left retina). In each LGN the projections from the two eyes terminate in designated layers, so that the topographic relationship of the two eyes are maintain (Meissirel et al. 1997; Erwin et al. 1999).

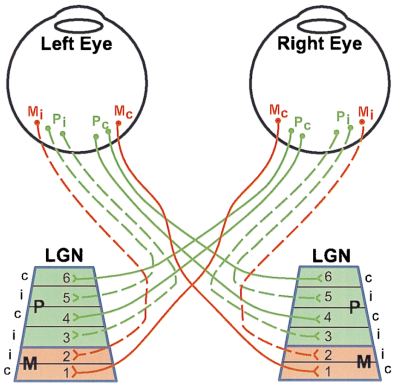

Figure 2-4 figure from Meissirel et al (1997, p. 5901) showing a schematic of the neuronal connections between the eyes and the LGN in the macaque monkey. c – contralateral; i – ipsilateral. Reprinted with permission.

Figure 2-1 illustrates a schematic from Meissirel et al (1997) where we can see that layers one, four and six receive the projections from the contralateral retina and layers two, three and five receive the projections from the ipsilateral retina. The reader is directed to Jeffries and colleagues' (2014) comprehensive review of the current knowledge of mapping of neural responses in the LGN. The axons of LGN neurons

will then project (forming the optic radiations) and terminate almost exclusively in layer 4 of the striate cortex, or the primary visual cortex, V1. The projections leaving the LGN orient to from a hierarchical order where, in the optic radiations, fibres from synapsed axons from the superior regions of the retina are located in superior portion of the radiations and vice-versa (Brazis et al. 2011). The optic radiations will thus carry information about the superior quadrants of the visual field (represented in inferior retinal quadrants) in the lower divisions that project along the temporal lobe and will carry information about the inferior quadrants of the visual field in higher divisions that travel the parietal lobe. The retinotopic organisation is maintained in the visual cortex. As can be seen in figure 2-2, the foveal region is represented in the posterior part of the visual cortex, whereas more peripheral areas are represented in progressively more anterior regions.

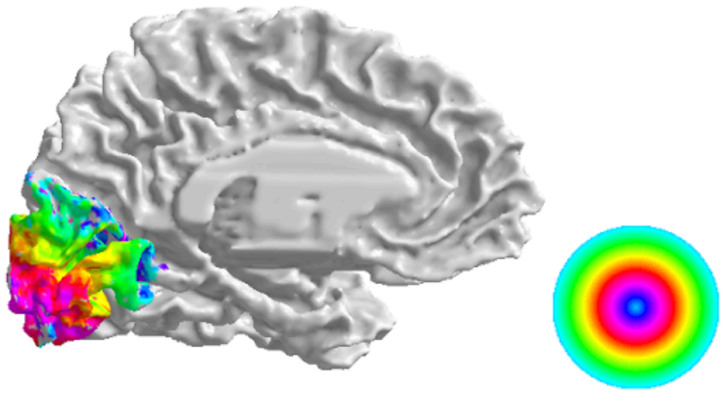

Figure 2-5 Figure adapted from Dougherty et al (2003, p.587) showing the retinotopic organisation in the visual cortex and the stimuli used to measure those retinotopic maps.

Although the retinotopic maps are preserved in V1, a much larger proportion of the visual cortex is dedicated to represent the foveal region. Other parts of the retinotopic map are greatly underrepresented in the cortex, a phenomenon termed by Daniel Whitteridge (1961) as the

cortical magnification, M. This distorted representation of the retina can be viewed in figure 2-6, below.

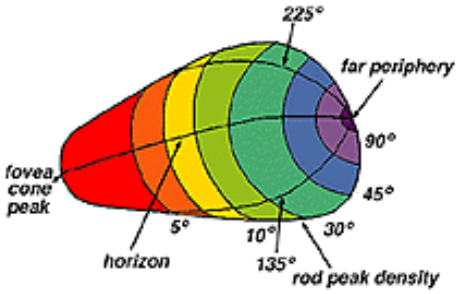

Figure 2-6 Unfolded striate cortex representing the cortical area used to represent the different parts of the retinotopic map. The fovea is greatly overrepresented in the cortex, while the periphery occupies less brain area. Figure from http://webvision.med.utah.edu/book/part-ix-psychophysics-of-vision/the-primary-visual-cortex/

2.2.2.1. Visual space beyond V1

As discussed in the previous section, two major streams are considered linking V1 to the inferior temporal cortex (ITC) and posterior parietal cortex (PPC). An influential study in monkeys has proposes a two stream model, much like what is had been hinted by Schneider a few years back (Schneider 1969): a dorsal stream, associated with spatial perception or object localisation, and a ventral stream, which has been linked to object identification and recognition (Mishkin and Ungerleider 1982). However, this view has been challenged by Goodale and Milner (1992) who proposed that the two streams do not exist solely to produce input distinctions of object location versus object features, but rather, they are involved in a much more complex functional network of the production of adaptive behaviour. Thus, a distinction between visual perception and visual action was born, giving rise to the perception-action model. Their observations of patient D.F. (a visual-form agnosia patient) and two other controls, led Goodale and Milner to propose that the (dorsal) visual projection to the PPC carry action specific information about the object's structure and

orientation and not just about its position in space. This information would ultimately be involved in spatial awareness, guiding actions such as reaching (Goodale et al. 1991; Goodale and Milner 1992). The ventral stream has been proposed to be associated with visual memory, awareness and visual cognition, but the spatial layout of the visual scene as well as the several features that identify objects and give them meaning concern both pathways (Goodale et al. 1991; Goodale and Milner 1992; but see Husain and Nachev 2007; or Schenk and McIntosh 2010).

Lastly, studies in monkeys have led to the discovery of several extrastriate areas also involved in the processing of visual information (Maunsell and Newsome 1987; Felleman and Essen 1991; van Essen et al. 1991). It was suggested that different regions are specialised in different aspects of visual coding, due to the response properties of the different neurons. For example, neurons in the area V4 respond to selectively to the colour of a visual stimulus while disregarding its direction of movement (Purves et al. 2004, pp 278). Alternatively, neurons in the middle temporal are (MT) respond selectively to the direction of movement of a visual stimulus, regardless of its colour.

2.2.3. **Auditory space**

The transduction process of hearing begins by converting air pressure into a wave-like displacement of the fluid in the cochlea that causes the movement of the structures in the cochlear ducts. In a simplified account, the movement of these structures[5] is then converted into

[5] Of particular importance are the basilar membrane and the organ of corti. As to not clutter the text with references, whenever not referenced, the information discussed here can be found in any textbook of the specialty. The author of this thesis refers the reader to two very well written books on the subject: Moore (2004) and Pickles (2008).

electrical potentials by the inner hair cells that travel to the auditory nerve and subsequence nuclei, on its way to the auditory cortex.

Unlike vision, examining the auditory pathway will tell us little about how the auditory system encodes space. Neurons in the cochlea are not tuned to regions of space like they are in the retina. We might consider that the auditory counterpart of this hierarchical (topographic) organisation that is found in the visual system is frequency, in the hearing system. The cochlea is tonotopically organised: high frequencies are represented fundamentally by neurons placed at the base of the cochlea near the oval window, and low frequencies by neurons at the apex of the cochlea. This orderly arrangement is preserved throughout the ascending stream and in the auditory cortex.

Of particular importance for sound localisation is a collection of brainstem nuclei called the superior olivary complex (SOC). The SOC can be thought of as a second stage auditory nuclei, before the signal travels to the inferior colliculus (IC), the medial geniculate body (MGB) and the auditory cortex (AC), and is preceded only by the cochlear nuclei (CN). At the SOC, the auditory stream is divided into two streams. One, a dorsal stream, is mainly concerned with sound identification, but the other, a ventral stream, is concerned with binaural sound localisation, and can be further divided into two streams.

In the first division, the intensities of the stimuli at the two ears are compared in a sub-nucleus named the lateral superior olive (LSO). The LSO is mainly populated by IE[6] cells, which means they are excited by ipsilateral stimuli and inhibited by contralateral stimuli (see Yin 2002

[6] Widely used terminology. IE refers to contralateral inhibited and ipsilateral excited. EE cell would be excited both by contra and ipsilateral stimuli.

for a review). This means that the LSO is able to extract interaural loudness differences (ILDs) in a frequency-dependant manner because at high frequencies, the intensity differences between the ears will be largest due to the smallest degree of diffraction of sound waves around the head. Most cells in the LSO are thus tuned to high frequency sounds (Caird and Klinke 1983; Tollin and Yin 2002). Moreover, a small contribution of a temporal delay in the inhibitory signal from the contralateral ear reaching the LSO, when compared to the earlier excitatory synaptic input from the ipsilateral ear, means that "the two effects summate to maximally supress the LSO responses when the stimulus is on the contralateral side of the head" (Pickles 2008, p. 176), although it has been shown that the contribution of the intensity effect is much larger (Park et al. 2004).

In the second division of the SOC ventral stream, the medial superior olive (MSO) is responsible for comparing the timing of the stimuli at the two ears. Contrasting with the cells in the LSO, the majority of the cells in the MSO are EE (contralateral excited and ipsilateral excited), although one-quarter of the cells are IE or EE. Furthermore, the MSO is almost entirely populated by cells tuned to low frequency sounds (Goldberg and Brown 1969; Brand et al. 2002). This is particularly important because, a sound source located at one side will stimulate the nearest ear first, due to the shortest sound path, but, for low frequencies, because of the wavelength, the phase difference between the two ears is unambiguous. By themselves, ITD (interaural time difference) and ILD cues can be ambiguous, and the use of further cues is needed from head movements and from the filtering properties of the pinna. More on this subject in the following section.

2.2.4. **Leading role of vision in spatial perception**

The area of choice to compare visual and auditory spatial maps has been the superior colliculus (SC)[7], since this structure holds spatial maps for each modality (reviewed in King 1999). Several lines of evidence point to the superiority of vision in spatial representation.

First, maturation studies in the SC suggest that it is the visual modality that guides the development of auditory maps. This has been shown in a series of studies in the barn owl (Knudsen 1985; Mogdans and Knudsen 1992) and in ferrets (King et al. 1988, 2000), by altering the spatial information available to the animals during development, but perhaps the clearest example of the leading role of vision comes from barn owl experiments using prismatic spectacles (Knudsen and Knudsen 1989, 1990; Knudsen and Brainard 1991; Brainard and Knudsen 1993; Feldman and Knudsen 1998). Figure 2-3 (below) summarises the results from these experiments. A barn owl wearing prisms that shifted the owl's vision in the horizontal axis by 23° to the right was trained to orient its gaze to auditory or visual targets. Before the prisms were mounted (top left panel; a) the visual and auditory responses coincided and were on target.

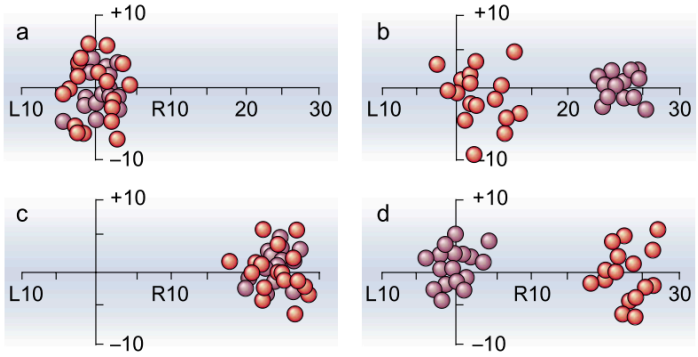

Figure 2-7 figure from Knudsen (2002) showing the stages of plasticity of auditory behaviour of a representative juvenile owl. Data is from Knudsen and Knudsen (1990). Auditory in red, visual in purple. a – before prisms were mounted; b – one day after prisms were mounted; c-

[7] or the non-mammalian counterpart, the optic tectum.

forty-two days of prisms usage; d – without prisms. Reprinted with permission (lic.: 3873030487182)

On day 1 after mounting the spectacles (top right panel; b), the visual responses were shifted to the right by the correct amount (23°) while auditory responses remained on target. Forty-two (42) days after continuous use of the right-shifting prisms, the auditory responses had shifted and were now adapted to match the visual responses (bottom left; c). Removing the prisms would cause visual responses to accurately track the target (right bottom panel; d) while auditory responses remained in the previous adapted location. This trend was further supported by neurophysiology investigations (Brainard and Knudsen 1993). Figure 2-4 depicts the ITD (interaural time difference) tuning of two single units, in the optic tectum of an owl reared with prisms. The response on the left (orange) was measured before prisms were mounted, while the red unit was measured after 8 weeks of prism experience. When prisms were removed, the red unit still showed ITD tuning to the shifted azimuth (despite both units having identical visual receptive fields).

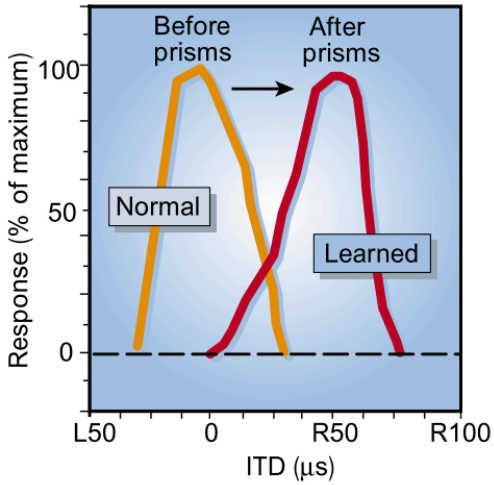

Figure 2-8 ITD tuning of two single units in optic tectum of owl reared with prisms (modified with permission from Knudsen, 2002; CCC lic.: 3873000758289.

The second line of evidence comes from anatomicophysiological observations: the superficial layers of the mammalian SC are exclusively dedicated to visual processing (Huerta and Harting 1984; review in King 1999), and spatial convergence with the other modalities (auditory and somatosensory) occurs only in the deeper layers (see Gutfreund and King 2012 for a review of the topic). SC neurons in the deeper layers respond to visual stimuli first (Wallace and Stein 1997), and the first neurons that respond to sound do not show any spatial specificity, responding similarly to a large region of space (e.g. King 1993). Additionally, maturation of the auditory spatial map in the deeper layers is hindered by visual deprivation (Withington-Wray et al. 1990).

The third line of evidence emerges from differences in sensory encoding. In the visual and somatosensory systems, the location of a stimulus source is directly encoded in the activity of each sensory receptors (in the retina or skin; 1981a, 1981b). For example, in the visual modality, the spatial maps in the brain result from topographic projections in the retina, maintaining its retinotopic organization throughout the ascending stream. The same is observed in the somatosensory system, where somatopicity is maintained throughout the afferent pathways (1981a). By contrast, in the auditory modality, the location of a sound is not coded directly in the cochlea; it has to be extrapolated from a set of acoustic cues. The fundamental cues that provide the basis for sound localisation include interaural time differences (ITDs; arising from the time difference it takes for the sound to reach the farthest ear) and interaural loudness differences (ILDs; arising from the attenuation of farthest the sound when travelling through and around the head; Moore 2004). By themselves these cues

can be ambiguous, as demonstrated by the "cone of confusion" (Blauert 1997), a phenomenon that emerges from presenting ILD and ITD cues alone: front-back or up-down localisations of a sound source (in one of the two hemifields) are confused due to equal ITD and ILDs in a conical area along an interaural axis. Additional information from head movements and spectral filtering (conveyed by the frequency--dependent directional properties of the pinnae) are needed to disambiguate further the location of the sound source (King et al. 2001). Thus, localising sounds based on hearing is not a straight forward encoding process by neurons specialised in a certain region of space (as it is in the visual modality). Further brain calculations are needed to deduce the location of a sound source. The function of the SC is believed to be aligning maps of space for the different modalities, however, it relies first and foremost on the visual modality, to do so (reviewed in King 1999; and Gutfreund and King 2012).

2.2.5. **Functional spatial performance**

Behavioural studies in humans also point to the spatial superiority of vision. In the auditory modality, the just noticeable difference in angular displacement that a listener can perceive (also termed as the minimum audible angle or the MAA), is around 1° in the horizontal and vertical plane, and is around 3.7° in the vertical plane (Perrott and Saberi 1990; but see Moore 2004). On the other hand, in the acuity literature of the visual modality, participants are able to discriminate spatial intervals between two lines as low as 8 sec (or arc) and a 2 to 4 sec of misalignment in a vernier task similar to the one described in this thesis (Berry 1948; Westheimer 1972, 1981; Westheimer and McKee 1977). This type of performance was termed hyperacuity by Westheimer and describes the higher level visual acuity in relation to

the more standard way to determine spatial-acuity by grating resolution tests (Geisler 1984; Gunilla Haegerstrom-Portnoy 2004).

For vision, performance is typically best at the midline and often decreases with eccentricity. This is especially true for static visual tasks that require a high degree of spatial resolution as it is with the vernier discrimination task presented in this thesis. For example, Golla et al (2004) investigated, in a series of experiments, the influences of spatial attention on the peripheral acuity threshold discrimination in humans and rhesus monkeys using a paradigm that required identifying a gap (either on top or on the bottom) in a Landolt 'C'[8]. The results show that performance was worse as eccentricity increased from 3° to 9° to 15°, for both humans and monkeys. However, for dynamic tasks, such as motion detection, performance is worse towards the midline, possibly due to the greater density of cell sensitive to motion (rods) in the peripheral visual field (McKee and Nakayama 1984)

2.3. ATTENTION

2.3.1. **Definition of attention**

For the purpose of this thesis, I will consider that attention is a mechanisms used by our brain to filter out unwanted "noise" in an attempt to enhance a given event of interest. Noise, here, is defined not as a sound or visual event, but anything that does not contribute in the event of interest. The very notion of attention supports the notion of a capacity limited brain, that is unable to process all the information of the outside world that our sensory system captures. The need to decrease the sensory sensitivity to unwanted or unimportant noise is crucial to leave some processing power to the task or attended event.

[8] Gap and size of 'C' was varied according to the individual adaptive performance

We will see in the pages that follow the overwhelming body of evidence to support this notion.

2.3.1.1. Early years of attention

Goal-driven or voluntary attention arises from individual preparations for the signal (Spence and Driver 1994). A participant might attend to the right side in anticipation of a signal appearing at the same location. If so, the participant will be faster responding than if the stimuli appeared in the opposite side. However, in the particular case of concurrent and interfering distractors, remaining focused in a goal--driven stimulus requires the use of what has been termed selective attention, which we might consider a particular case of voluntary attention. Selective attention will be particularly important in chapter seven, where participants are required to attend to one side and discern from a broadband noise target, the presence (or not) of an amplitude modulation in the noise, while concurrent visual or auditory stimuli will be presented.

The booming of selective attention studies began in the auditory modality, and can be traced back to the early 1950's with Edward Cherry's (1953) experiments of dichotic listening. Cherry's research was focused on the "cocktail party" phenomenon, an ability to extract relevant conversations in the midst of multiple conversations entering our ears at the same time. In one of Cherry's experiments, "a continuous spoken message was fed into a headphone on the subject's left ear and a different message applied to the right ear" (p. 977). The participants were able to extract the attended ear message with no difficulties, however, participants could say little about the message in the unattended ear, "except possibly that sounds were occurring" (p. 978). Further manipulations of the unattended ear revealed that

participants were unable to identify any words or semantic content, or being absolutely sure if the message was in English, but were able to identify male speakers from female ones. Encouraged by these finding and others (Broadbent 1952, 1954, Poulton 1953, 1956) that showed that separation of the source and pitch differences of voices were needed for message selection, Donald Broadbent (1958) published the filter theory. In his book, the nervous system was viewed as a single channel that receives all the information available to the senses, in parallel. From here, the information is held momentarily in a buffer (short-term memory) before filtering[9] and being sent to further processing. Information that is not selected is lost. In this model, the process of selection was considered to rely on the physical attributes of the stimuli (intensity, pitch, source location).

This model was almost immediately challenged by Moray (1959) who found that participants were able to recognise their own name in the unattended stream, however, it was the work of Treisman (1960)[10] that initiated a series of studies that ultimately led to the development of a late selection model by Deutsch and Deutsch (1963), which accounted for the semantic effects at the unattended ear. They proposed that selection would come later, after the information had been fully processed (semantic analysis and weighted for importance) before being selected for awareness. The debate between early and late selection models was born, and a surge of selective attention studies flooded the attention literature on the two decades that followed Deutsch and Deutsch's (1963) publication. Treisman went on to put

[9] Needed due to the lack of processing resources by later stages

[10] In her study she showed that by switching an attended story to the unattended ear participants followed a few words at the unattended ear before switching back to the attended ear.

forward a model of selective attention during visual search, reusing ideas from the filter theory: that physical features are processed in parallel and at an early stage. The FIT (feature integration theory; Treisman and Gelade 1980) proposed that the physical features of the stimulus are registered early (and automatically) and in parallel, across the visual field, "while objects are identified separately and only at a later stage, which requires focused attention" (p,98). Thus, colour, location, direction of movement, orientation and brightness are coded serially and attention is needed to "glue" or integrate these features into an object that is then stored in memory. Without focused attention the physical attributes cannot be related to each other (Treisman and Gelade 1980; but see Wolfe 1994). The original FIT was fairly criticised[11] and quickly replaced with updated versions of the theory (and Duncan and Humphreys 1989 model; such as the guided search model, Wolfe 1989). Finally, a publication by Lavie and Tsal (1994) proposed a resolution to the early/late selection debate by suggesting that selection of information depends on the available system capacity, which in turn is modulated by the perceptual load of the task. Selection of information under the load theory is accomplished passively in conditions of high perceptual load (since there is insufficient resources to process distractors, Lavie and Tsal 1994; Lavie 1995), and actively (by using higher cognitive functions like working memory to reject irrelevant distractors) in conditions of low perceptual load (Lavie et al. 2004).

[11] For example, Tsal (1989) questioned if illusory conjunctions, general taken the basis for the FIT, truly support Treisman theory. Furthermore he heavily criticizes the vagueness of the "glue" that holds features together into objects.

2.3.1.2. Attentional modulation

Our sensory system is systematically bombarded by information from the surrounding environment. However, the capacity of the visual system to process all the information available in a given instance is very limited (when compared to the amount of information available Broadbent 1958; Schneider and Shiffrin 1977; Shiffrin and Schneider 1977). A simple task can be used to exemplify this limited capacity system: when participants are asked to report two different features of two different objects that appear at the same time (e.g. colour and orientation), the performance is worse than if only one object is presented (Treisman 1969; Duncan 1980, 1984). Thus, it is natural that due to the limited resources, multiple events that are presented simultaneously compete for neural representation in the brain (Kastner and Ungerleider 2000). There are several processes that the brain uses to resolve the competition between multiple objects in the visual scene. One, for example, depends of stimulus properties, as in finding the vertical line inserted randomly in the midst of several horizontal lines, or finding a blue square in the middle of several red circles. These are stimulus driven or bottom-up processes and depend on stimulus salience to bias the competition towards the most salient object (Treisman 1969; Treisman and Gelade 1980; Duncan 1984; Duncan and Humphreys 1989; Kastner and Ungerleider 2000). However, in other cases it is not possible to resolve the competition solely on the basis of object salience, and in the event that the target shares many features with surrounding objects, making its saliency very low, the brain can resort to bottom-down processes (such as spatial attention) to bias the object competition. One example of this is cueing the participant to a region of space where the target will appear (Posner 1980). In this case,

spatially directed attention will enhance the processing of information at the attended site. This will be covered in detail in the pages that follow (and in particular in section 2.1.4 "Attention to space").

Studies in monkeys (Moran and Desimone 1985; Reynolds et al. 1999) and later (Kastner et al. 1997, 1999) have enabled us to understand the neural correlates of this competitive stimuli interactions. It seems that neural responses show a weighted average that each individual stimulus would present in isolation. So, for instance, if one stimulus elicits a high firing rate whereas a second stimulus presents a low firing rate, the averaged response when the two are presented simultaneously is reduced in comparison with the higher firing rate of the first stimulus (Moran and Desimone 1985). The two stimuli interact in a way that the overall response is suppressed, not added. This suppression has been interpreted as an outcome of the competition for neural resources (Kastner and Ungerleider 2000). As mentioned above, this competition can be biased by stimuli salience in a bottom-up fashion but also by top-down processes such as attention deployment. Biasing inputs due to selective attention can result in several neural processing outcomes. One, the enhancement of neural responses to the attended stimulus has been observed in single cells when an animal (monkey) covertly directs attention to a stimulus within the neurons receptive field (RF), in comparison to when the animal attends outside of the receptive field of the neuron (Spitzer et al. 1988; Motter 1993; Connor et al. 1996; Luck et al. 1997). Two, there is evidence that the top-down modulation of neural signals can be accomplished by increasing the baseline firing rate to an attended location, without the need for visual stimulation (Colby et al. 1996; Luck et al. 1997; Kastner et al. 1999). For example, Luck and colleagues (1997) have shown that the stochastic firing rate of neurons

in areas V1 and V4 of macaque monkeys shows an increase of 30 to 40% to when attention was directed inside, rather than outside, of a cell's receptive field, "even when no stimulus was present in the receptive field" (Luck et al. 1997, p24). Third, to compensate the suppression resulted from the competition by nearby distractors filtering of unwanted information is possible by means of spatially directed attention. Reynolds et al (1999) measured the responses of Macaque monkeys in the areas V2 and V4 and found that directing attention to a stimulus inside a neuron's RF removed the suppressive impact that a second stimulus, presented in the same RF, would have. The authors also compared this effect to when attention was directed outside the neuron's RF and found that the effects of attention were less pronounced, thus suggesting that attention may resolve competition of nearby distractors at the attended site and that competition is stronger within the cell's RF (but see Kastner and Ungerleider 2000,p 323, for a review of this and other fMRI studies). Lastly, attention allocation to a stimulus increased V4 neurons sensitivity by 30%. Furthermore, this effect was especially noticeable in low contrast stimuli (Reynolds et al. 1997). The increase of a neuron's sensitivity to stimulus contrast will ultimately increase the stimulus saliency, a contributor to resolving the object competition, as we saw above. According to Kastner and Ugerleider (2000) " the stimulus that wins the competition for representation in visual cortex will gain further access to memory systems". Next section I will briefly revise the interaction between memory and attention.

2.3.2. **Attention and memory**

One of the most popular models for studying memory is the three stages model proposed by Atkinson and Shiffrin (1968), depicted in the figure 2-9, below.

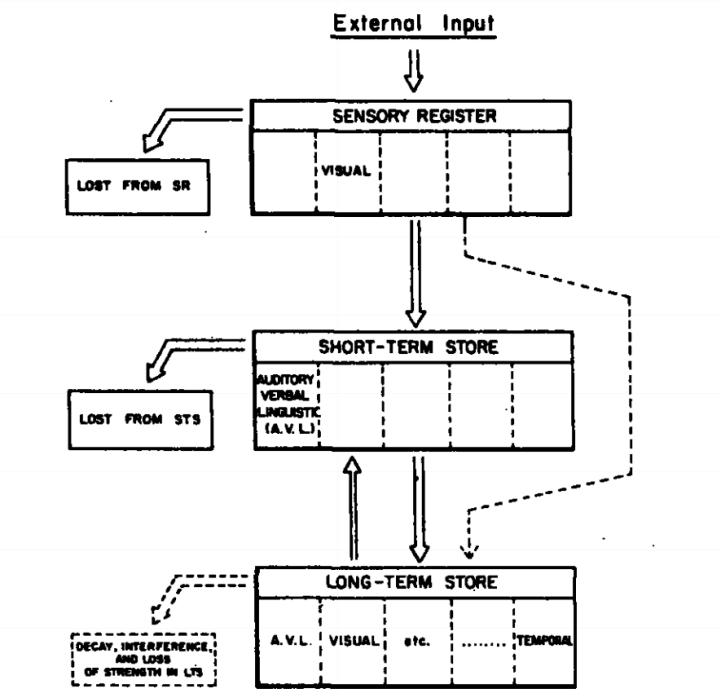

Figure 2-9 Atkinson and Shiffrin (1968) proposed system of human memory. This is also known as the modal or multi-store model of memory, in which three stages are involved in the creation of long term memories.

According to this model, forming a memory can involve three active stages of information encoding. The first stage is sensory memory, lasting usually less than a second, and it can be divided according to the human senses. Thus, the sensory memory for auditory stimuli is called echoic memory, the visual counterpart is called iconic memory (the touch, hepatic memory, etc). Information passes from sensory memory to short-term memory, which lasts less than a minute and is often also referred to as working memory. From here information is consolidated in long-term memory that can last for a life time.

In summary, sensory memory is the ability to maintain sensory information that is no longer present in the environment (Sperling 1960). But, to ascend from sensory to the short-term memory stage, attention control processes filter that information. If we contrast sensory memory (the ability to retain information that disappeared from the environment) to the general definition of attention, which is the ability to discriminate and target information that is present in the environment, one can begin to understand why often sensory memory and attention are considered to be discrete processes. However, currently there is enough evidence to suspect that these two phenomena are related and share common resources. For example, it is now clear that attention plays a significant a role in both early sensory selection and postperceptual maintenance of information in working memory (Awh and Jonides 2001). The notion that attention influences the storage of information in working memory has been studied actively since 1994, when Smyth and Scholey (1994) proposed that covert shifts in spatial attention helps maintaining information in working memory (see Awh et al. 2006 for a comprehensive review on attention and working memory). There is also compelling evidence that attention tends to move towards the location stored in the working memory (Bisley and Goldberg 2003). It appears that it is attention that will determine which events will be given a space in the limited capacity working memory and that the mechanisms recruited in the active maintenance of information within special working memory are the same processes that "*facilitate the early sensory identification of new information*" (Awh et al. 2006, pp 207). Another study shows compelling evidence that spatial visual attention is the mechanism behind both the integration of information in working memory and its retrieval (Theeuwes et al. 2011). The practical outcome of these

interactions seems to be that people with a higher working memory capacity also exhibit a better ability to direct attention to a target while ignoring surrounding noise (Awh and Pashler 2000; Awh and Jonides 2001; Awh et al. 2006).

2.3.3. **Attention to space**

It is currently established that there are two distinct ways in which attention orienting to space can be achieved. One, head turning and saccadic movements (classified as overt attention orienting) aim to bring the object of interest into the foveal space, where visual acuity is highest. Overt orienting have been studied extensively over the past decades and a wide range of findings attested the importance of hearing in overt orienting localization tasks (a nice review of this topic can be found in the introduction and general discussion of Spence and Driver 1997). In summary, orienting your head, or even foveating a salient stimuli by means of a saccade, is perhaps the most consistent behaviour resulting from hearing a sudden sound (e.g. Thompson and Masterton 1978). This reflex is also found in newborns and infants and is, in the present day, used in clinics for hearing assessment of infants up to 5 months old (for instances in BOA, behavioural observation audiometry; see McCormick 2004 for a detailed review). Posner (1980) defined orienting as "the aligning of attention with a source of sensory input or an internal semantic structure stored in memory" (p.4) and raised the possibility of a second kind of attention orienting: a shift in attentional focus accomplished without any visible postural adjustments (covertly). In covert orienting, attention is moved elsewhere without retinal movements, in which case the foveated object is not the sole object of attention. Unlike overt attention where eyes can only be oriented to one location at a time (thus is serial in nature) covert

attention has a parallel nature since it can be deployed to more than one region in space (Carrasco 2011). For example, as I write this thesis, the UEFA European 2016 championship in newspapers and television is a daily presence. The game of football is a great social example of the importance of covert attention, where tracking an opponent without deviating the gaze from the ball makes players aware of the spatial disposition of the opponent team, and of possible lines of pass when own team players advance through the field. The same covert attention would have been crucial in a war context, or even in hunting, where awareness of the position of other members of their own party is imperative, while not loosing track of the prey (foveated).

The general consensus is that covert attention precedes eye movements, allowing us to monitor our spatial environment, and guiding gaze in finding the location of a salient and/or relevant event (see section 3 of Carrasco 2011). There are currently three broad explanations (or models) of how covert attention increases spatial performance. Sensory enhancement, noise reduction and efficient selection models are usually supported by different authors, but Marisa Carrasco (2011), in her comprehensive review of visual attention in the 25 years preceding her publication, proposes that these are not mutually exclusive. The author adopts the notion that performance reflects a combination of the three mechanisms, since "all three are likely to contribute to the computational processes by which attention improves performance" (p.1489). The sensory amplification or "gain control" model predicts that information that is attended elicits larger neural responses and thus increases the S:N (signal-to-noise ratio) in comparison to unattended information. The gain control or amplification modulation process of attention has been reasoned in a variety of experiments, from EEG and

MEG (Hillyard et al. 1995, 1998), to PET (Corbetta et al. 1990, 1993; Heinze et al. 1994) and psychophysics (Hawkins et al. 1990; Hikosaka et al. 1993; Tsal et al. 1994). A second model, the reduction of external noise (either by noise exclusion or distractor supression, Carrasco 2011) predicts that attention reduces the influence of concurrent external noise by either acting like a filter in a specific location, allowing only specific information to pass (noise exclusion) or by allowing the observer to use a filter and disregarding other filters that carry unwanted information from outside the locus of attention (distractor supression; Dosher and Lu 1998, 2000; Lu and Dosher 1998). Lastly, as the spatial uncertainty and the number of distractors increases, performance decreases (see e.g. Baldassi and Burr 2000; or Cameron et al. 2002). Cues presented at a spatial location will enable observers to effectively select a region of space to focus their search for the target stimulus, thus reducing the spatial uncertainty (Davis et al. 1983; Palmer 1994; Nachmias 2002). This way, noise from unattended locations is reduce, thereby also increasing the S:N. The next section will cover the two fundamental types of covert attention, exogenous and endogenous orienting.

2.3.3.1. Types of covert attention

Covert orientation can be accomplished by two means: exogenously (or automatically), produced by external stimuli in a bottom-up manner; and endogenously (or voluntarily), triggered by individual expectancies in a top-down fashion (Corbetta and Shulman 2001; Klein 2004; but see Funes et al. 2005 and; Prinzmetal et al. 2005). Endogenous attention is also referred to as "sustained" attention (in comparison to exogenous that is often referred to "transient"). This terminology refers to the temporal time-course of the two effects. Endogenous attention

takes around 300 ms to be deployed and can be sustained in the location of the target for as long as it takes for the participant to complete the task (Carrasco 2011). Conversely, transient attention rises and dissipates quickly (under 300 ms). The faster time course of exogenous attention has also been supported by single-unit recordings in the extrastriate area MT of the macaque cortex (Busse et al. 2008).

When an unexpected event occurs in the periphery of the foveated field, such as an abrupt sound or light, our sensory system tends to orient the focus of attention towards the location of that new event (Yantis and Jonides 1990). The behavioural effects of exogenous attentional orienting are well known. For instance, targets presented in the same location of a previously presented attention grabbing cue are detected faster (Posner and Cohen 1984; Eriksen and James 1986; Posner and Petersen 1989). Moreover, flashing a cue at the same location of a target letter (displayed immediately after) will increase the accuracy of its detection (Eriksen and Collins 1969a; Eriksen and Rohrbaugh 1970a). The authors showed that this accuracy increased with stimulus onset asynchrony (SOA) until it reached a maximum performance at around 200 ms of SOA and then levelled off. Colegate and colleagues (1973) using a similar multiletter display task validated these findings by reporting the same increase in performance during the 200-250 ms window, however this time using reaction time measures (these measures have long been linked to attention facilitation; Posner 1980). Further attention benefits can be seen at attended locations, where spatial resolution is higher (He et al. 1997), and contrast (Carrasco et al. 2008; Carrasco 2011) and luminance sensitivity (Hawkins et al. 1990) is lower than in non-attended locations.

We have seen that exogenous attention benefits typically occur when the target is presented within 200 ms of the cue, after which, attention is withdrawn from the exogenous event (Eriksen and Rohrbaugh 1970a; Eriksen and Hoffman 1972, 1973; Posner and Cohen 1984). In both endogenous and exogenous conditions, the processing benefits are identical: detection of a target is faster and more accurate in cued locations than in uncued ones (Posner 1980). However, after this, when a new sensory event "appears" at the same location (after 200ms), attention deployments to this location are now slower in comparison to deployments in a new location. This phenomenon was termed inhibition of return (IOR; Posner and Cohen 1984; Posner et al. 1985). The attentional facilitation observed within the first 200 ms of cue-target onset asynchrony (CTOA) is reversed for the next three to six seconds (Samuel and Kat 2003; Tipper et al. 2003; Dodd and Pratt 2007), presumably to give priority to novel locations over previously inspected locations (see Klein 2000; or Dukewich 2009, for a review).

Jonides (1981) observed that, despite the benefits of cueing near the probable location of a target, moments before the appearance of a target character amongst seven other letters, when the cue occurred at non-target locations, there was a significant cost in processing time and in accuracy in identifying the target letter. When directing attention it usually understood that the focus of attention is also the locus of interest. However, as observed by Jonides, there are situations when attention is automatically drawn away from the locus of interest. This notion that attentional shifts also produce costs at foveated locations is the fundamental reasoning behind the attentional repulsion effect (ARE), detailed in the next section (2.4 Mislocalising space).

2.3.4. **Mislocalising Space**

Orienting is a necessary step in directing attention (Spence and Driver 1997). The sensory benefits of orienting the focus of attention have been extensively researched in the past decades, and are currently well established. In summary, facilitation is observed to events (targets) occurring at the same location as an attention-grabbing cue. As seen in the previous section, this facilitation has long been characterised in exogenous attention: higher spatial resolution, faster reaction times and increased accuracy. Exogenous attentional effects show a gradual increase in perceptual performance until a certain point where performance will either stabilize or decrease, however, despite the overwhelming quantity of studies in attention, not much is known about the benefits or the costs of (unimodal and crossmodal) attentional deployment when the region of interest is not the same where the exogenous event occurred. Thus, a sudden exogenous deployment of attention to an unimportant location might neglect the main location, causing a perceptual bias. In fact this has been shown in the past, albeit only in unimodal visual conditions (Suzuki and Cavanagh 1997; Pratt and Arnott 2008).

Focusing attention on a preceding visual cue can cause changes in the perceived lateral position of a subsequently presented visual target. This effect was demonstrated almost two decades ago, where participants were asked to judge the lateral displacement of one vertical line relative to another (vernier display paradigm). Suzuki and Cavanagh (1997) described this as “attentional repulsion” and it has been studied exclusively in the visual domain. Importantly, this paradigm shows for the first time the influences of a peripheral distractor (that draws attention to itself) on the spatial perception of

another visual object (the object of interest) that is placed in a different location (where fixation is on-going).

2.3.4.1. A review of the attentional repulsion effect (ARE)

In its basic method, participants were asked to fixate a cross at the centre of the screen, after which a cue circle was flashed briefly (30 ms) in diagonally opposite quadrants: either on the "top-left + bottom-right" or "top-right + bottom-left". After a stimulus onset asynchrony (SOA) of 180ms, two vertical lines (one above and one below the fixation cross; in a vernier display) were flashed for 60ms, followed by a random-dot mask screen (250ms). Participants were asked to judge the lateral displacement of the top vertical line relative to the bottom line. When the diagonal cues were on the top right quadrant, participants reported an offset in the counter clockwise direction, and when the cues were in the opposite quadrant, a clockwise shift of the target was perceived. The perceived misallocation of a target stimulus in a direction that is opposite to the transient exogenous cue was termed attentional repulsion effect (ARE). Participants reported that covertly directing attention to sides (left or right) would cause a repulsion of the top vernier line, away from the location of the cue. Suzuki and Cavanagh (1997) termed this as the "attentional repulsion effect" and it has been studied extensively in the visual domain. The authors reported a repulsion effect of around 10 arcmin (0.16 degrees of arc), and other studies reported similar numbers (5.5 arcmin or 0.09 degrees, Kosovicheva et al. 2010; 0.101 degrees Ono and Watanabe 2011).

In the original study, seven experiments tested this effect under several conditions. The results indicate that the repulsion effect did not increase significantly by increasing the distance between the cue and the target

and the authors ruled out non-attentional hypothesis by testing the ARE against figural artefacts (a one second adaptor circle opposite to the transient cue did not alter the repulsion of the target by the transient cue) and apparent motion from cues to target[12]. Additionally, attentional influences gained further support when the authors observed the presence of the effect under voluntary attention conditions. It is well known that transient stimuli capture attention at cue locations and that this process is involuntary. Studies have shown that visual acuity and sensitivity improves momentarily with transient spatial cueing (see for instance Nakayama & Mackeben 1989 and Hawkins et al. 1990) but, similar enhancements have also been demonstrated with voluntarily attention (for review see Carrasco 2009). Suzuki and Cavanagh (1997) postulated that if the repulsion effect is due to attention, then endogenous attention should induce the same effect. In fact, the effect was present in tasks where participants were controlled for voluntarily attending the side of the cue. The magnitude of the reported effect seemed, however, smaller than that for the exogenous induced repulsion. Under involuntary attention the repulsion effect decreased as a function of SOA after 200ms, reaching a steady state at around 800ms, although, the authors only tested two participants and remains unclear if these are trained participants or if in fact a bigger sample would behave in the same manner. Nakayama and Mackeben (1989) who describe the time course of sustained and transient components of visual attentional shifts demonstrated that the accuracy of vernier discrimination at cued locations also changes as a function of SOAs improving until it peaks at around 200ms and steadily

[12] the repulsion effect was not a two-frame version of the representational momentum as the motion distractors included in the same frame as the vernier test were travelling in the direction opposite to the repulsion effect

declining thereafter. Interestingly, both studies show a sustained effect that lasts for at least 1400ms (Suzuki & Cavanagh 1997; Nakayama & Mackeben 1989). Both authors argue that attention was grabbed by transient stimuli and was sustained until a next event. When compared with the transient cue-induced repulsion, the voluntary-induced repulsion effect took longer to rise significantly above zero (120ms, as opposed to 30ms of the cue-induced repulsion). The 90ms difference was interpreted by Suzuki and Cavanagh (1997) as the time taken for the observer to recognise the shape and voluntarily attend to it. Nevertheless, the specific time-course of the ARE is open to debate, a topic that this thesis addresses in chapter six.

2.3.4.2. Manipulating the ARE

When investigating the spatial relationship between the locus of interest (the vernier at the centre of the screen) and the locus of attention (the exogenous visual cue at the sides), Suzuki and Cavanagh (1997) found that the attentional repulsion effect was independent of the distance between cue and target (tested distances were 2.1°, 4.9° and 7.7°). This was not supported by Kosovicheva et al. (2010), who tested larger distances, and found an inverted u-shaped curve of the bias as a function of cue-target distance, with 2° to 8° as the distances with bigger mean bias effects (~7 arcmin; 0.12°) and 0° and 12° with the smallest mean bias (5 and 3 arcmin approximately; 0.08° and 0.05° respectively). Kosovicheva and colleagues (2010) further investigated if the spatial distortion of perceived location of the vernier lines is due to spatial attention or attention to object contours and found that attention is attracted to the centre of mass (an empty location within each cue). Furthermore, simultaneously increasing the size of the cues and distance between the centre of mass and the vernier lines did not

increase the size of the ARE. Together with the finding that when the centre of mass is held constant, increasing or decreasing the size of the cue does not alter the size of the ARE, it seems that it is the distance between the cue's centre of mass and the vernier lines that determines the size of the ARE (Kosovicheva et al. 2010).

The ARE was also studied under colour manipulations. Gozli and Pratt (2012) presented participants with a modified ARE paradigm in which the cues were either red or green open circles and the targets were five fixed lines above and below the fixation point. One line on top and one line on the bottom would differ in colour from the rest of the lines matching or mismatching the cues. The ARE was observed by both targets that matched and mismatched in colour. The fact that Gozli and Pratt (2012) found an ARE independent of the cues matching in colour with the targets suggests that mislocalisations of space happen regardless of the voluntary deployment of attention (which is a top--down control process). However, studies of the ARE that report endogenous deployments of spatial attention fail to directly show the connection between a repulsion of a target by a lateralised cue and the voluntary attention deployment. When instructing the subject to attend to a red circle or a green square, the attention of the subject is being scattered over the entire possible space, not localised to one side or the other. Additionally, in Gozli and Pratt (2012) the uncertainty of the target stimuli was weakened by presenting all of the possible locations of the target (5 lines) always at the same place at the same time (with only variations of colour).

Yamada et al. (2008) reported that spatial mislocalisation judgements also happen when a target is preceded by a subjective or a luminance contour stimulus. The participants observed a task-irrelevant (Kanizsa's

subjective or luminance contour) cue displayed in the upper left or right visual field alongside with a no contour stimulus in the opposite upper visual quadrant. Target positions were mislocalised towards the luminance or subjective contours. Trials with the no-contour stimulus did not show a perceptual position shift of the target form 0^{o}. Displacement errors varied between 0.30^{o} and 0.45^{o}.

2.3.4.3. Underlying mechanisms and locus of the ARE

Suzuki and Cavanagh (1997) suggested that the effect originated in the primary visual cortex (also supported by Nakayama & Mackeben 1989) and explained the results in view of three theories: the surround suppression, the receptive field (RF) recruitment and the receptive field shrinking theories.

2.3.4.4. The three theories of the ARE:

If we assume that the position of an object in space is represented by the centroid of the overall response distribution of a population of position--coding neurons (figure 2-10) , then reducing the spike rate at one of the tails of the population distribution can positively or negatively skew it. This is the very basis behind the three theories proposed by Suzuki and Cavanagh (1997) to explain the ARE. When a vernier is presented at the centre of unit's 4 RF, this unit will respond the most. Other units further away from the location of the vernier will respond less until the last two units in figure 2-10 (units 1 and 7) whose tuning curve does not intercept the location of the vernier, present no activity (other than the stochastic firing rate – baseline).

Since the position-coding units have receptive fields that are spatially tuned, the sum of all the receptive fields of the position-coding units span the entire visual field.

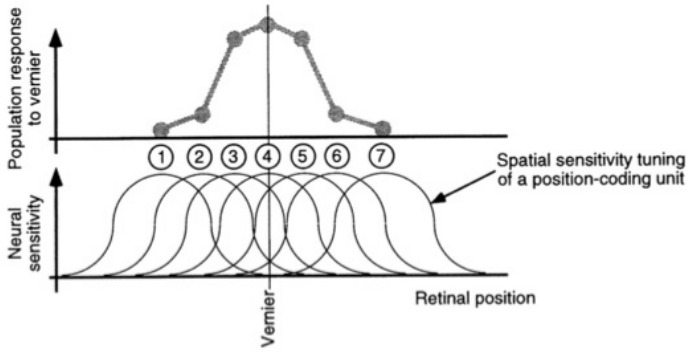

Figure 2-10 Seven hypothetical position-coding units and their respective neural activity in response to a vernier presented at the centre of unit's 4 RF. From Suzuki and Cavanagh (1997)

This asymmetry from the population distribution will invariably alter the distribution's centroid giving rise to an altered perception of space. The three theories share a common end result which is the fact that recruited units respond less to stimuli away from the centre of attention either by increased tuning of the RF of units near the site of attention, or by RF shifting to represent the site of attention or by inhibition of surrounding units to those whose RFs are in the centre of the attended site (Suzuki and Cavanagh 1997).

Suzuki and Cavanagh explain the three proposed hypothesis: " the first possibility is that the activity of the cells surrounding the focus of attention is suppressed perhaps via lateral inhibition – the surround suppression hypothesis (Suzuki and Cavanagh 1997 p 458).

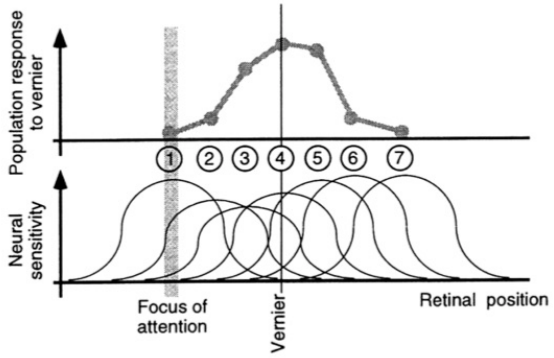

Figure 2-11Surround suppression theory, from Suzuki and Cavanagh 1997. Check text.

In this hypothesis, figure 2-11, attention is located at the centre of the RF of unit 1. In response to this attention focus, the surrounding units decrease their firing rates (Suzuki and Cavanagh suggested that perhaps lateral inhibition is at play). As a result of this inhibition, the centroid of the overall response curve shifts to the right, thus the vernier will appear slightly shifted to the right, explaining the perceived repulsion. In the second proposed theory the RF recruitment hypothesis, figure 2-12, the neighbouring cells to the location of the attention (unit 1) shift their receptive fields to enhance perception at the attended site. This leaves less units to represent the vernier location causing a shift of the overall distribution to the right, explaining the repulsion percept, as before.

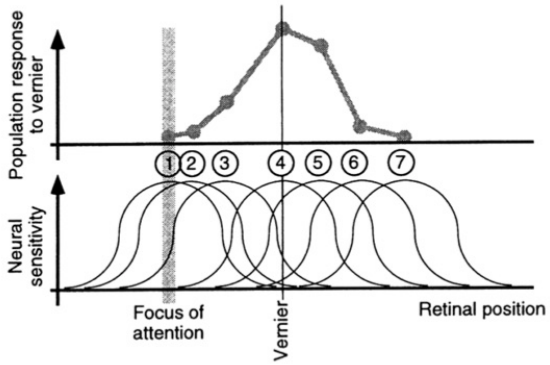

Figure 2-12 RF recruitment hypothesis behind the ARE by Suzuki and Cavanagh, 1997.

Lastly, in the sharpening or tuning of RF hypothesis, figure 2-13, focused attention sharpens the RF of units in the centre of the attended location, thus resulting in reduced responses to the vernier, which in turn would shift the centroid of the overall distribution to the opposite side.

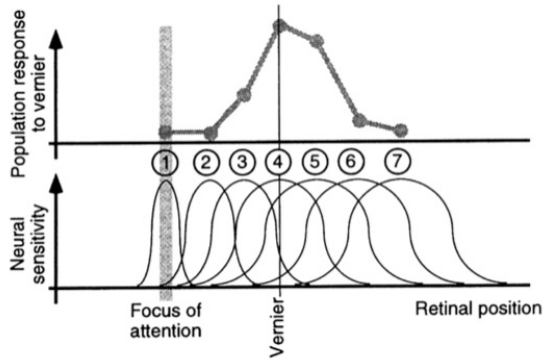

Figure 2-13 RF shrinkage hypothesis by Suzuki and Cavanagh, 1997.

One of the questions that this thesis raises is the possibility that the ARE can be a multimodal phenomenon. If attentional shifts are truly in the centre of this effect, and assuming attention is a crossmodal phenomenon (see Driver and Spence 1998b for a review), then I would predict that moving the ARE to another modality should yield the same repulsion (albeit with effect size differences due to the intrinsic nature of each stimuli). But, one must contemplate that the theories presented here for the explanation of the ARE might not be transferable to modalities that do not code space in the same manner, as in the auditory modality, for example. In the auditory modality, space is inferred through calculations during the binaural processing. This means that the level where the three theories operate (low peripheral level – retina neurons) is different in the auditory modality and as such, it would be difficult for these theories to apply to the auditory modality. This topic will be discussed further in the General Discussion chapter.

In an attempt to determine the locus of the ARE effect, DiGiacomo and Pratt (2012) measured the effect in both monocularly and binocularly conditions and assessed the interocular transfer by presenting the cue to one eye and the target to the other eye. Results from the visual conditions (mono and binocular) were of matching sizes, suggesting

that the use of one eye only did not compromise the ARE. This suggested there was no need for binocular visual processing to be present, therefore, the authors concluded that the ARE most likely results from monocular receptive fields of cells somewhere before V1 (the first stage of the visual system where cells are tuned to binocular differences). Furthermore, the interocular condition did not show an ARE, which supports the notion that this effect is likely to happen quite early in the visual processing stream. If binocular processing was at the centre of this effect, then presenting cues and targets to different eyes would not matter as the information would later be joined (after V1; DiGiacomo & Pratt 2012), leading to an intact ARE. Furthermore, Pratt and Turk-Browne (2003) were able to replicate the attentional repulsion effect (with reported biased values of 0.4^{o}) and found that this effect affects perception and also action. Using a guided localisation task (where participant had to move a computer mouse and position the cursor where they thought the top vernier target was) and a guided limb localisation task (participant now responded to the top vernier line target location by touching the screen with the index of their dominant hand) the authors reported that pointing responses were biased even though the participant were able to discriminate between all vernier targets (for instance, the touch accuracy was very high, on average participant touched -11.6 pixels for the -12 vernier target, -6.2 for the -6 and -0.8 for the 0). Pratt and Turk-Browne (2003) suggested that the effect originates relatively early in visual processing, arguing that it must be instantiated before the visual signal segregates into their ventral and dorsal streams. Thus, to affect both perception and action, it must be carried down both visual pathways.

Whether it is attention that solely underlies the ARE is not known, but studies have shown that this effect is very sensitive to attentional manipulations. It is known for quite some time that cueing enhances spatial discrimination (see for example Nakayama & Mackeben, 1989). Other consequences of allocating attention in a specific region of space are the faster and more accurate processing of information. For instance, lower detection thresholds and more accurate detection of objects are observed at attended locations as opposed to unattended locations (e.g. Hodgson & Muller 1999; Henderson 1991; Pratt & McAuliffe 2001). The same attentional manipulations that modulate response times (RTs) where studied in the context of the ARE (Pratt and Arnott 2008). If spatial distortions brought upon by transient exogenous cues are in fact due to attention, then by using those conditions that are known to produce effects in RTs should also modulate the ARE. In other words, Pratt and Arnott (2008) investigated if attentional changes that yielded greater RTs would yield greater AREs as well. Here is important to clarify what cues the authors have used, that are known to produce attentional effects in RTs. There are three types of cues: onset, onset-offset and offset cues. So far we have discussed peripheral attentional manipulations using exogenous cues, but in fact, these cues have an onset (associated with their appearance on screen) and an offset (associated with their disappearance), so can therefore also be called onset-offset cues. This is to distinguish from cues that appear and remain on screen (onset cues) and cues that suddenly disappear and do not reappear (offset cues). Pratt and McAuliffe (2001) studied these three types of cue and observed that all of them produced RT attentional cueing effects of the same magnitude (targets at cued locations were detected faster). In Pratt and Arnott's study (2008) abrupt onsets that appeared in all four corners should not yield a

repulsion effect, but the fact that one of the four isoluminant cues differed only in colour repulsed the targets prompted the authors to support the notion that mislocalising space is truly due to shifts of attention. This is because stimuli that differ significantly in one or more attributes from their context (that are subjectively salient), are able to capture attention in a bottom-up manner (see Egeth & Yantis, 1997, for a review). Pratt and Arnott (2008) also observed a correspondence between temporal (as measured by RTs) and spatial effects (as measured by the ARE), which suggests that RTs and AREs attentional processes could be linked: onset, onset-offset and offset cues produced attentional repulsion effects. Furthermore, the magnitude of the effect was not significantly different across cue type.

2.3.4.5. Attentional attraction effect (AAE)

In the previously reviewed studies, attention was shifted away from the location of a vernier target, presented before (or at the same time) as the visual cues. Ono and Watanabe (2011), asked whether orienting attention after the presentation of the vernier target would also alter the perception of repulsion. In their study, Ono and Watanabe manipulated the ISI between cue and target (like the original ARE study by Suzuki and Cavanagh), however, they extended the interval to the time after the target has been presented. Thus, the authors tested thirteen ISIs, six with the cue presented before the target (negative ISI values) and six after (positive ISI): -700, -400, -200, -100, -50, -20, 0, 20, 50, 100, 200, 400, 700. In a first experiment, the authors saw that if the cue was presented before the target, participants reported the top vernier line to be displaced away from the location of the cue. This result was in line with the ARE literature and, in the same manner, it peaked around 200 ms of

ISI and disappeared when ISIs were longer than 400 ms. However, when the cue was presented after the target, participants now reported the target to be shifted towards the location of the cue. This attentional attraction effect (AAE) peaked around 200 ms and was resolved in ISIs longer than 400 ms. In a second experiment, Ono and Watanabe aimed to investigate if the effect was truly due to attentional shifts, thus, the authors presented simultaneously left and right diagonal cues, however, only one of the diagonals was relevant to the task. Participants were asked to attend to squared or circled cues, or to red or green cues[13]. Misjudgements in the targets' locations (both attraction and repulsion) were only attributed to attended cue pairs. In other words, spatial distortion was concluded to be due to attention shifts (evoked/exogenous or focused/endogenous attention). The authors reported attentional biasing effects of approximately 0.15 degrees (for repulsion) and approximately 0.10 degrees (for attraction). They also observed that the focused attention bias was smaller than the exogenous attention (approximately 0.1 degrees for repulsion and 0.025 for attraction). Ono and Watanabe (2011) argued that the position--coding units hypothesis proposed by Suzuki and Cavanagh (1997) cannot account for the fact that the direction of the effect (attraction or repulsion) depends on whether the target is presented before or after the cue.

It remained unclear if a single mechanisms underlies both attraction and repulsion effects. To answer this question, Chien et al. (2011) examined the interaction between the attraction and repulsion effects.

[13] in a first experiment, the shape was the feature to attend, so, participants either attended to top-left-bottom-right or top-righ-bottom-left squared cues. In a second version of this experiment, participants attended to the colour, regardless of the shape of the diagonal pair.

In a first experiment, participants were presented with a cue-target and a target-cue condition that replicated respectively the repulsion and attraction effects (0.054° of repulsion and 0.096° of attraction). In all experiments, the SOA was maintained at 200ms since Ono and Watanabe (2011) had previously shown that repulsion and attraction peaked at 200ms around the target. Following this, the authors examined the interactions caused by cues preceding a target (leads to repulsion) and cues following a target (leads to attraction) by having cues presented before and after the target in the same trial. The hypothesis was that if preceding and following cues have independent influence on the lateral judgements, then the resulting bias would be a sum of the negative repulsion and the positive attraction values (-0.054°+0.096° = 0.042°). Because the attraction was slightly higher than the repulsion in the previous experiment, Chien et al. (2011) postulated that a small attraction would result from the addition of these two values. A dependant relationship between attraction and repulsion would yield values that would differ from the simple sum of both effects. The results show that, in fact, spatial distortion was close to the simple summation of repulsion and attraction (0.045°), thus implying an independent influenced by preceding or following cues. By presenting a cue simultaneously with the target, and another one before or after the target frame, Chien et al. (2011) found that the attraction effect was diminished but no apparent change was observed on the repulsion effect. This is consistent with the idea that attraction is caused by a dynamic attentional shift of the target to the cue (Ono and Watanabe 2011). Since Suzuki and Cavanagh (1997) attributed the repulsion to an attentional focus on the cue at the beginning of the trial, Chien et al. (2011) hypothesised that repulsion and attraction might have different

underlying mechanisms (static attentional focus and dynamic attentional shift, respectively).

In a study by Yamada et al. (2011), participants were asked to judge the spatial position of a target in relation to a probe, under several cue--target and target-probe asynchronies (similar to the classic ARE by Suzuki and Cavanagh 1997). Here, however, the authors varied the temporal relationship between target and probe in a first instance, using 0ms, 500ms and 1250ms. They found that the attentional repulsion observed at 0ms was not present at 500ms and turned into an attraction with the increase of the target-probe SOA to 1250ms. To complement these results, the authors tested when the attentional repulsion vanished and for how long did the attentional attraction lasted by implementing a series of SOA between target and probe (8 SOA; 0, 100, 200, 400, 600, 1000, 1600, and 2000ms). Results show that repulsion is strongest at around 100-200ms and attraction lasts until the last SOA of 2 seconds. Furthermore, they simultaneously varied the SOA of cue-target and target-probe to study the temporal dependency of the repulsion and attraction effects, respectively. They used 3 target-probe SOAs: 0, 500 and 2000ms (repulsion was observed at 0ms, attraction at 2000ms and no interaction at 500ms). Cue-target SOAs were: 50, 200, 1000, 1500ms. Results suggest that for the cue-target SOA of 200ms and 1000ms, the repulsion effect changes to an attraction as a function of the temporal difference between target and probe (where an interval greater than 600ms was necessary to observe repulsion). Main effects of cue-target SOAs and target-probe SOAs were significant, but not their interaction suggesting that delays between cues and targets affect localization independently of delays between target and probe. Because Yamada and colleagues (2011) found attention-induced perceptual

distortions at SOAs of 2000ms, the authors speculated that the perceived location of the target remained in memory (short-term) and can be subjective to further attention induced spatial distortions (attraction). In other words, the repulsion effect is perceived when target and probe are presented simultaneously but, with longer intervals, the perceived location of a probe is compared to a target preserved in memory. The authors stated that repulsion can happen in the earlier stages of visual processing, but attraction may occur in later stages in the memory.

Zimmermann et al. 2013 reported visual attractions when delays between two significant visual events ranged between 68ms and 200ms, after which the effect would vanish. They also reported shifts in spatial perception by as much as 4^{o}. It would appear that transient stimuli grab the attention within 200ms after which endogenous cues would have to be deployed to maintain attention. This is also supported by Nakayama and Mackeben (1989) who found that performance varies dramatically depending on the interval between cue and targets. It took 50ms for a leading cue to promote a rise in performance. Target discrimination rose steeply after 50ms of cue leading time and was best at around 80-100ms, falling off after 200ms.

But, attention shifts are not always accompanied by visual awareness. They can also be drawn unconsciously by presenting cues below the observer's visual awareness (Mulckhuyse et al. 2007), but what is the role of visual awareness in the ARE? Au et al. (2013) developed a masked and unmasked cue paradigm to answer this exact question and demonstrated for the first time that the retrospective effect of attention shown by Ono and Watanabe (2011) in modulating spatial perception can also occur without spatial awareness. In other words, imperceptible

visual cues can also induce attentional repulsions and attractions. But, Au et al. observed that the size of the repulsion effect is significantly larger for unmasked conditions (observers can identify if cue was presented on the left or the right quadrant) than for masked conditions (observers could not identify which side the cue appeared on the screen). In a follow-up experiment, the authors required observers to judge both target and cue positions in an attempt to study if the attraction and repulsion effects are in fact associated with the physical position of the cue (which is masked, therefore it is an unconscious attentional deployment) and not with the reported position of the cue (guessed by the observer). Although, performing a target and cue (double) judgement task weakened the repulsion and attraction effect, Au and colleagues were still able to observe that the ARE was primarily based on the physical (yet unaware) position of the cue and did not occur with the participants reported cue location (guessed). This suggests that attention modulation of spatial representation is not necessarily associated with visual awareness (Au et al. 2013). However, the authors did not provide any evidence that attention was being drawn by the cues in the masked conditions and thus, the ARE could also be due to non-attentional mechanisms. Despite this, the substantial attenuation (values reported are in "percentage of right responses" and therefore it is not possible to have an idea of the size of the bias) of the repulsion and attraction from unmasked to masked conditions suggest that the effect is possibly potentiated by attention and awareness. It seems, also, that there is no main effect of the target position on the attraction or repulsion effect. Both left or right targets have been shown to induce the same bias (Au et al. 2013).

2.3.4.6. Mislocalisations due to crossmodal interactions

A significant amount is known about visual, auditory, audio-visual or visual-auditory[14] spatial perception. Two fields of science are usually associated with crossmodal studies. One, the basic and fundamental science that investigates neuronal and single cell behaviour. The other is concerned with the perceptual outcome of this sensory competition and/or cooperation. Regarding the first field, in appendix one we can see how a single cell, residing in a once believed specialised portion of the cortex (the auditory cortex), can in fact represent other modalities. For instance, the auditory cortex has the remarkable potential to represent vision from birth, even without any sensory deprivation (Yaka et al. 1999; Bizley et al. 2007) and continues to reshape its function long after its phylogenetic source of stimuli (sound) has cessed (Buonomano and Merzenich 1998; Lomber et al. 2010; Dormal and Collignon 2011; Meredith et al. 2011). The prevalence of bimodal and unimodal visual cells in A1 was shown (in appendix one, and by Bizley et al. 2007) to be significantly less than specialised auditory cells, in cortices with normal function. However, even though there is an overwhelming body of literature on crossmodal convergence and integration at the neuronal level (see e.g. Meredith and Stein 1986; Stein et al. 1988, 1989; Wallace et al. 1993; Meredith 2002), it is possible that these processes could refer to the basic characteristics of cell physiology. Perception is the final stage where all the inputs from a myriad of sensory epithelia come together, and this is influenced not only by bottom-up processes (e.g. spontaneous or exogenous deployment of attention) but also by top-down processes (e.g.

[14] Distinctions are needed since the sequence of events in time is vital for perceptual fusion. Thus, the adopted nomenclature is that the modality of the first event is named first in the pair.

expectation and voluntary deployment of attention). The perceptual construct of an environment starts with specialised receptors that send information up. Information is changed as it ascends along the cognition stream[15], thus, it is possible that the first stage coding at the neuronal level differs from the actual percept of the outside world.

Studies on spatial perception following crossmodal stimulation can also be divided into two subgroups: automatic crossmodal processes that influence spatial perception and crossmodal spatial attentional processes. The overarching theme of the present thesis is the perception of space following attentional shifts, but of partial relevance is the ventriloquism effect, discussed in chapter four. The ventriloquism effect is a visual-auditory spatial conflict that results in an automatic misrepresentation of space. It is named after the illusion ventriloquists create (Howard and Templeton 1966): the speech that they produce without articulatory movements from their lips appears to be coming from a puppet that is moved simultaneously. This is one case where visual information dominates over auditory spatial information in the perception of the location of an object. The ventriloquism illusion is not exclusive to the puppet/ventriloquism scenario and other uninformative or neutral cues (flashes and tones) will also result in a ventriloquism illusion (e.g. Bermant and Welch 1976; Radeau 1985). In these laboratory-like conditions, the ventriloquism illusion is characterised by an attraction of auditory targets towards the location of preceding visual cues, and is stronger in locations where localising auditory cues is poor (Slutsky and Recanzone 2001). Conversely, in conditions of blurred visual cues over a large region of space, it is the audition that captures vision (Alais and Burr 2004a, 2004b). Lastly,

[15] Or rather, the plural, streams, since multisensory convergence exists to unify inputs from the several sensory pathways resulting in a useable percept.

crossmodal attentional mislocalisations of space have been reported in line with the ARE phenomenon in the visual modality. The crossmodal ARE was investigated by Arnott and Goodale (2006). The authors saw that visual repulsion effects can also be elicited using lateralised sounds. Arnott and Goodale adapted the original ARE paradigm (Suzuki and Cavanagh 1997) replacing a visual cue with an auditory cue (broadband noise) coming from three speakers positioned above (upper middle) and to the sides of a computer screen (left and right). The authors reported similar results to Suzuki and Cavanagh's study, but interestingly, auditory effects remained smaller than those observed with the visual cue. Since the ARE is thought to arise from cue-induced bias in retinotopic neurons in early visual areas (Pratt and Turk-Browne 2003; DiGiacomo and Pratt 2012), these results suggest that lateralised sounds can influence the retinotopic response of the visual cortex despite eye movements not accounting for the attraction or repulsion (Arnott and Goodale 2006; Yamada et al. 2008).

2.3.4.7. Could sensory adaptation contribute to the ARE?

> *"Some fifty years after the first physiological studies of auditory attention, the field is now ripening, with exciting recent insights into the psychophysics, psychology, and neural basis of auditory attention."*
>
> (Fritz et al. 2007a, p.437)

Figure 2-1 shows the number of publications produced in a recent PubMed search (June, 2016) with the terms "visual spatial attention" or "sensory adaptation" or "auditory spatial attention" in either the title or the abstract, per year. Spatial attention yielded over 8,000 publications (visual = 7459; auditory = 1123) while sensory adaptation generated over 6,000 publications.

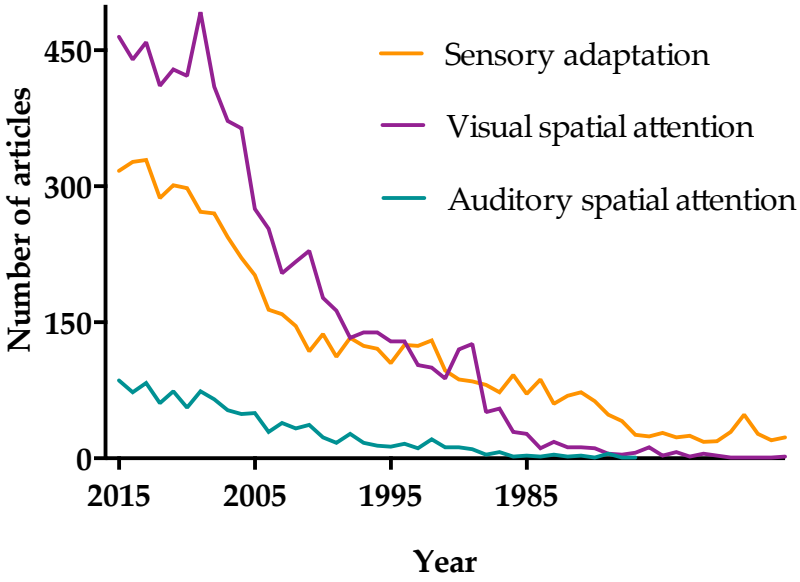

Figure 2-14 Number of articles per year in a PubMed search.

Considering that spatial attention and sensory adaptation are both sub--specialties of larger scientific fields, the growth in the number of publications in both topics, in the last 50 years, is remarkable. Nevertheless, despite the growing interest in such specialised fields, the effects of spatial attention and sensory adaptation are recurrently studied separately. Seldom is the case where studies investigate the combined effects of attention and sensory adaptation, despite most psychophysics paradigms (such as the ARE), repeating the same stimuli thousands of times, uninterruptedly.

Dahmen et al, (2010, p.937) states that "to use the neurons' limited dynamic ranges more efficiently, adjustments in coding strategy can be made throughout life and within seconds or milliseconds of encountering a change in the composition of the sensory input". Since the sensory nervous system, regardless of its efferent input (somatosensory, auditory, etc), is known to depend on past stimulus experience and is able to change its response properties with sustained stimulation, it is surprising that sensory adaptation is often not

considered as a possible intervenient. Evidence for adaptation can be found at all stages, from single unit recordings (e.g. Kadohisa and Wilson 2006) to large neuronal structures (e.g. auditory cortex Lanting et al. 2013) and perception. (e.g. Whitaker et al. 1997; but see Kohn 2007, for a review). In the attention domain, psychophysical studies within the visual modality, using a variety of spatial tasks, point to the behavioural effects of attention. Some studies have reported improvements in target selection out of an array of competing stimuli, due to attention deployments (see e.g. Treisman 1980; Duncan and Humphreys 1989; Wolfe 1989), while other studies described attention facilitation (increased accuracy, quicker responses) in the processing of a single stimulus at the attended location (e.g. Posner 1980; Reinitz 1990). In the auditory modality, focusing attention in a sound produces identical effects as the ones observed in the visual modality. For instance, sound-focused attention speeds up auditory processing as seen in the temporal studies of the prior-entry effect[16] (see Spence and Parise 2010 for a review); while segregating simple targets[17] from noise is done more efficiently when attention is deployed to the target (e.g. Ahveninen et al. 2006; however, see the introduction of Fritz et al. 2007b, for a short summary of the auditory attention field; Okamoto et al. 2007). Behavioural evidence suggests that attention facilitates the attended stimuli or attended locations while filtering events occurring at unattended sites. This motivates the question whether attention can influence adaptation, when directed to the adapter stimuli, and how.

[16] In this effect, attended sounds (or sounds presented at attended locations) are perceived earlier than unattended ones.

[17] Narrow-band noise, as opposed to complex stimuli, such as speech, as illustrated in one of best known examples of auditory attention: "the cocktail party effect" (Cherry 1953)

A common approach to study sensory adaptation in the auditory modality is to manipulate the mean and standard deviation of the stimulus statistics of the overall distribution from which the individual stimuli is selected (Chander and Chichilnisky 2001; Dean et al. 2005; Garcia-Lazaro et al. 2007; Maravall et al. 2007; Dahmen et al. 2010), although skewness and kurtosis have also been used in the past (Kvale and Schreiner 2004; Bonin et al. 2006). Dahmen and colleagues (2010) investigated the effects of adaptation on spatial perception, using a paradigm that bears many similarities with the ARE paradigm, and manipulating the mean and standard deviation measures of the adapter[18], mentioned above. In their study they found that attending to an auditory adapter (presented either at the left or right) would repulse the auditory targets (presented in the centre) that followed. I question that if attention facilitates the attended stimuli, would attending to an adapter increase the size of the reported repulsion?

A study by Rezec, Krekelberg and Dobkins (2004) has already hinted to this possibility, although not in the auditory modality, but in the visual modality. The "motion aftereffect" (MAE) phenomenon is perhaps the most studied psychophysical effect in the visual modality (1998; but see Rees 2001, for a short review of the topic). This phenomenon refers to illusory movement of a stationary scene following prolonged exposure to a visual motion scene. The direction of motion of the stationary scene is perceived to move in the opposite direction of the motion scene and is believed to reflect the adaptation of direction-selective neurons in area V5/MT (Tootell et al. 1995). Rezec et al (2004) showed that the MAE effect lasted longer when the participant was actively attending to it, thus suggesting that attention enhanced the adaptation produced by

[18] A detailed description of this paradigm can be found in the introduction of chapter seven.

the motion scene. Figure 2-2 depicts a representative participant of this study.

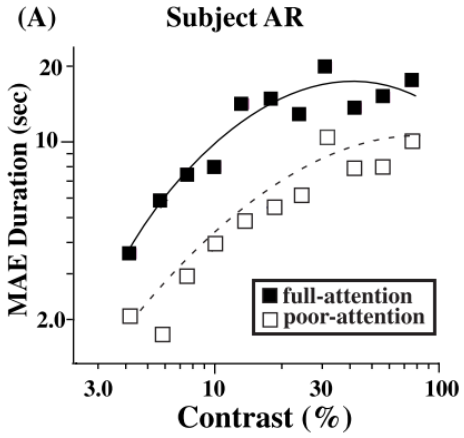

Figure 2-15 Example of a representative participant from Rezec et al (2004). License number 3867100721941, from CCC.

The MAE field of research is, however, very active, and conflicting evidence is published frequently. For example, prior to the above 2004 study, Rees (2001) stated in his preview of a Neuron issue: "However, in this issue of Neuron, Huk and colleagues (Huk et al. 2001) present provocative new findings that will force a reconsideration of this interpretation. Their new findings suggest that V5/MT activation during the MAE may be entirely accounted for by the participant' enhanced attention or arousal during perception of illusory motion." (p. 6). Despite uncertainty being evident regarding the putative neural substrates behind the MAE phenomenon, it is also reasonable to speculate that, in this case, both adaptation and attention may have their share of influence, making it harder to disentangle the contributing weights of one from the other. In cases like this, it helps to have a notion of what the role of one phenomenon is, over the other. Thus, in chapter seven, I set to investigate the combined effects of attention and adaptation in an auditory spatial task, which to my knowledge, has not been proposed before.

2.4. SUMMARY

When a growing number of laboratories began to the study attentional orienting in the beginning of the 1980 decade, scientists were fast to realise that out of other physical properties of the stimulus (e.g. offset transients, Yantis and Jonides 1984; e.g. hue, Jonides and Yantis 1988; Miller 1989), abrupt onsets of changes in luminescence were particularly robust in generating exogenous attentional orienting. In this literature review we have seen extensive evidence regarding the effects of exogenous attention on spatial discrimination. These can include decreased reaction times or increased accuracy at attended locations (Colegate et al. 1973; Rezec et al. 2004; but see Carrasco 2011, for a review), but, this facilitation occurs only if the targets are within 150-200 ms of ISI. After this window of facilitation attention is slower to return to the already searched locations, a phenomenon termed inhibition of return (IOR). Despite the significant amount of studies on the benefits of allocating attention to a particular region of space, less consideration has been given to the consequences of this allocation in the perception of other regions of the space, and as such these effects are more poorly understood. One field of science that investigates perceptual spatial errors due to allocating attention away from the region of interest is the ARE literature. In this literature review we contextualised the ARE within the exogenous attention literature. In the original study by Suzuki and Cavanagh (1997), the authors asked participants to judge the lateral displacement of a vertical line relative to another (in a vernier display), presented in the centre of the screen, when followed by a visual probe presented at the sides. The ARE is characterised by a repulsion of the top vernier line away from the location of the flashed visual cue, and is thought to result from the

overshoot of attentional shift from cue to target (Shim and Cavanagh 2004; Yamada et al. 2008; Ono and Watanabe 2011). We have also seen the ARE strongly associated with attentional processes. First, Suzuki and Cavanagh (1997) ruled out figural and representational momentum artefacts. Second, if the ARE is due to attention, then the effect should be observable with exogenously and endogenously deployments. In fact, this was shown by Suzuki and Cavanagh (1997) and confirmed by Ono and Watanabe (2011). Third, the ARE is strongly sensitive to manipulations of attention (Pratt and Arnott 2008). However, a question was raised (section 2.4.3) whether attention solely underlies the ARE or if adaptation due to repetitive presentation of the paradigm also contributes to the phenomenon. This question will be addressed in chapter seven.

A final note on the concept of attention: the reader would have notice that nowhere in this review is a well-defined account of what attention is. This can perhaps be attributed to the omnipresence and often paradoxal nature of the attentional system. A web search for "attention" on Google yields the following definition: *"notice taken of someone or something; the regarding of someone or something as interesting or important"*[19], while dictionary.com defines it as "*the act or faculty of attending, especially by directing the mind to an object"*[20]. The difficulty to describe the concept of attention may rise from the fact that it is not a single concept attributable to a single phenomenon. It is the name for a myriad of psychological phenomena, ultimately expressed in the several niches for attention research (spatial

[19] Google (28 June 2016), retrieved from https://www.google.co.uk/#q=attention

[20] Dictionary.com (28 June 2016), retrieved from http://www.dictionary.com/browse/attention

perception, object selection, feature integration, working memory, etc). It is not surprise that, to some, definitions of attention are often avoided (Styles 2005), and that to others, there seems to be an inherent ability to know what attention is. In 1890, Williams James wrote in his book entitled "The principles of Psychology": "*Every one knows what attention is. It is the taking possession by the mind, in clear and vivid form, of one out of what seem several simultaneously possible objects or trains of thought. Focalization, concentration, of consciousness are of its essence. It implies withdrawal from some things in order to deal effectively with others, and is a condition which has a real opposite in the confused, dazed, scatterbrained state which in French is called distraction, and Zerstreutheit in German".* In this thesis I have adopted Talsma and colleagues' (2010) notion of attention, stated in their review of multisensory attention: "*attention is an essential cognitive function that allows humans and other animals to continuously and dynamically select particularly relevant stimuli from all the available information present in the external or internal environment, so that greater neural resources can be devoted to their processing*" (p. 402).

This thesis will pursue the aims of understanding how extrapersonal space is maintained or altered in the presence of surrounding irrelevant stimuli (either in the same modality or in a different modality) that will exogenously pull attention away from the location of interest. In the next chapter I will focus on methodological aspects, including the research design, data collection, and data analysis.

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CHAPTER 3 GENERAL METHODS

3.1. INTRODUCTION

The general methods chapter contains information about the materials used in this thesis that are common to the psychophysical experiments 1 to 6. It also contains general common procedures for calibration, data collection and data analysis. This chapter will begin by describing the experimental set up and stimuli, followed by details of the procedure and data collection. Next, information regarding the pre-processing of the behavioural data (such as psychometric fitting and exclusion criteria) will be described. The appendices related to this chapter will contain the matlab code of all the psychometric functions used in this thesis.

3.2. MATERIALS

All experiments and offline data processing were conducted using a PC machine running a commercial software package (MATLAB 7.9, The MathWorks Inc., Natick, MA, 2000). Experimental stimuli were controlled using the Psychophysics Toolbox Version 3 (PTB-3) extension (Brainard 1997; Pelli 1997). Figure 3-1 is a photograph of the experimental set-up. Visual stimuli were displayed on a 60 Hz, 17″ colour monitor (16.7 ms refresh cycle) with 1280x1024 pixels of resolution and drawn against a black background (0.1 cd/m^2), placed in a in a dark acoustically treated room. A chin rest with a forehead support ensured the participant's head was fixed at 45 cm from screen. Auditory stimuli were presented through two speakers (VISATON FX 10 – 4 Ohm) positioned at a horizontal azimuth angle of 32.8° from the centre of the screen and 6.4° above the centre of the screen. Linear

stereo panning with a 6dB SPL dip in the centre was applied to compensate for the loudness summation at this location.

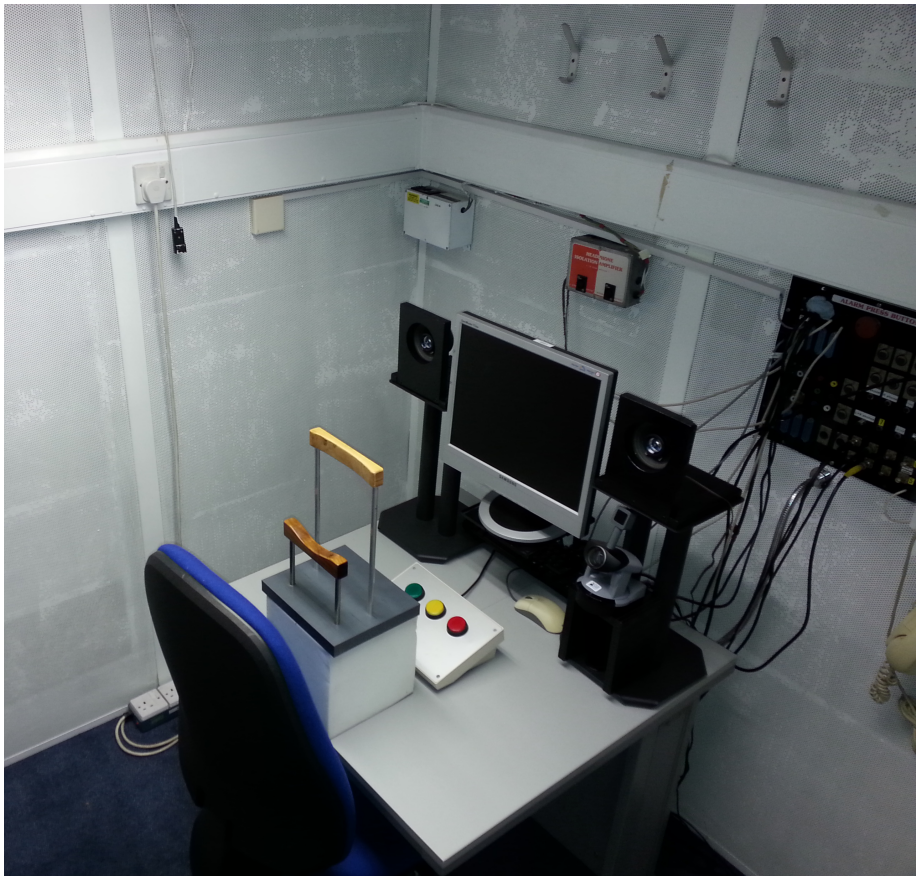

Figure 3-1 Prototype of experimental set up in a soundproofed room. Chin rest and response box was fabricated in-house. Speakers were later enclosed in a custom built closed baffle to minimise the effects of wave cancellations.

3.2.1. **Eye tracking system**

An infrared eye tracker (SMI RED system 3), running in a dedicated computer with an old version of the Microsoft NT operating system Windows XP (2001), was used to confirm if fixation was maintained in a dot displayed in the centre of the screen. It was essential to control for eye movements since there is considerable evidence that saccades influence both visual (Ross et al. 2001; Morrone et al. 2005) and auditory (Razavi et al. 2007) spatial perception. The eye tracker system uses two features of the eye to measure eye motion over time, the centre of the pupil and the first Purkinje image of the corneal reflection. Calibration

was required in order for the system to "learn" how the eye behaves when it's fixating in known locations. For this, calibration consisted in displaying 9 targets (open white circles) to which the participant must fixate (figure 3-2) while the system monitors the eye. Calibration of the eye tracker was performed in every session before running the behavioural experiment. In certain cases, tracking the eye position became problematic when disruptions to pupil capture or interferences with the corneal reflection were present.

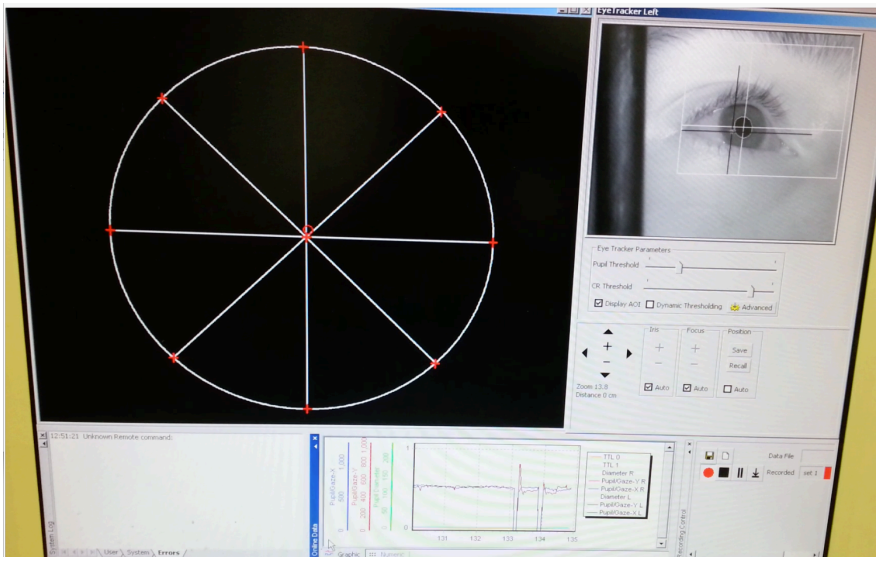

Figure 3-2 – Eye tracker system calibration. The upper left of the screen denotes the position of the targets displayed to the participant in random sequence. The upper right denotes the eye tracker parameters that adjust the pupil and corneal reflection threshold and window of operation. Below is a live tracking of the eye displayed in a graphical format.

This was the case, for instance, when the participant was wearing glasses (figure 3-3; top), where black areas tricked the system into misjudging the pupil position and reflections from the frames caused a corneal reflection misreading. Other cases that can cause a position misreading include the use of eye mascara and/or of contact lenses. Additionally, if a participant moves from its original position (figure 3--3; left) after the calibration of the eye tracking system, the subsequent reading will appear misleading. This occurred frequently since participants often adjusted their head or neck to find a more

comfortable position in the chin rest, however, it did not meant the participant was not fixating in the centre of the screen. Rather, it constituted one of the limitations of such system. The eye tracker was used in-situ to monitor the participants' eye position during the behavioural session. In cases where the participant was not fixating where it was instructed to (either by saccadic movements or by closing the eyes), the session would be interrupted, further instructions were given and the experiment would be restarted.

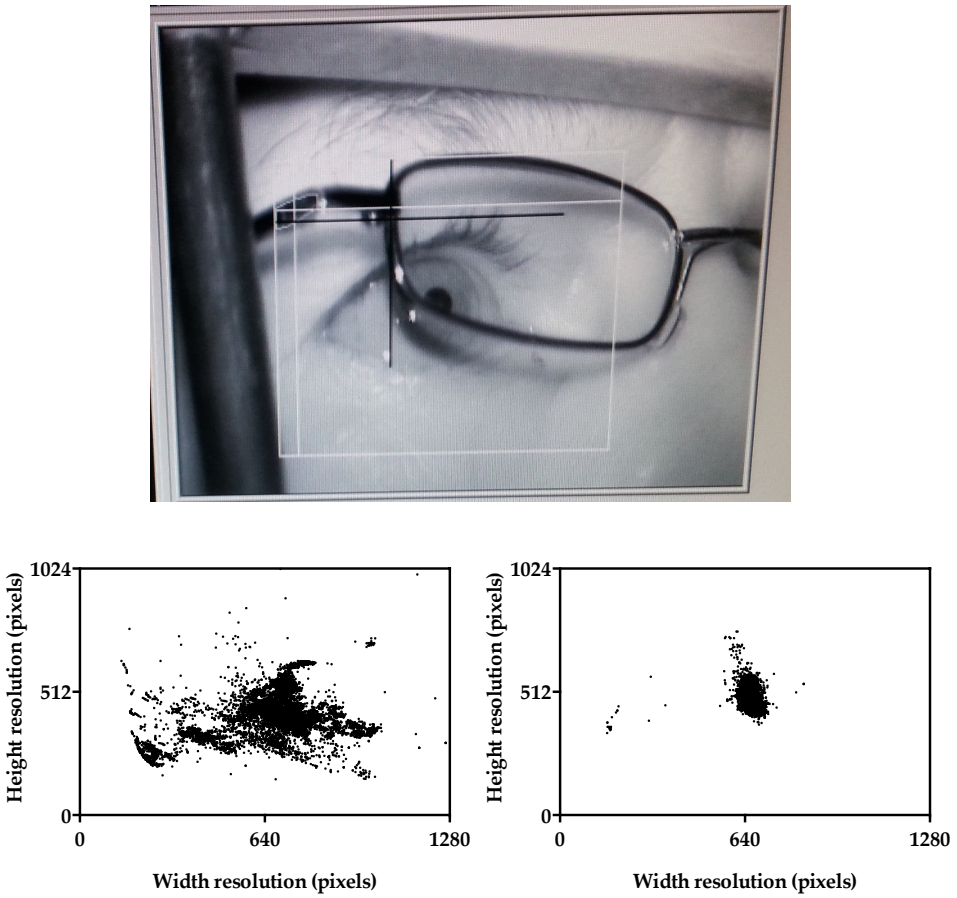

Figure 3-3 Eye tracking error. Top – Readings of pupil (black cross) and corneal reflection (white cross) are misguided by contrasts from the frame of the glasses. Bottom left – erroneous eyetracking data from one session where participant had good corneal and pupil calibration but frequently changed the head position during session. Bottom right – example of good eye tracking session where dots are clustered around the centre of the screen. Scattered dots represent blinks. Axis dimensions are the same as the computer monitor (resolution 1280x1024 pixels).

3.3. GENERAL PROCEDURE

3.3.1. **Participants**

Participants were naive to the purpose of the study. Before being included in the study, an auditory assessment (using the British Society of Audiology pure tone audiometry standard procedure) comprising a five-frequency audiometry (250 Hz, 500 Hz, 1 kHz, 2 kHz and 4 kHz) was performed. Participants were required to have normal hearing and normal or corrected to normal vision. Figure 3-4 shows the average hearing thresholds for experiment 2 and a representative participant of experiment 5. Participants were tested individually and provided informed consent prior to inclusion in the experiment.

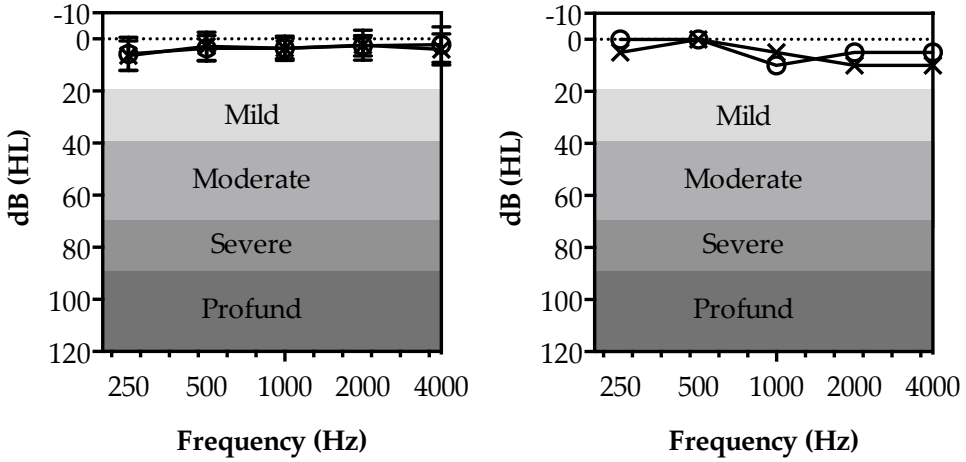

Figure 3-4 Example of hearing thresholds established by a pure tone audiometry. Left - average hearing thresholds of experiment 2. Right – representative participant of experiment 7. Frequencies tested were: 250Hz, 500 Hz, 1kHz 2kHz and 4kHz. Error bars show SD. Shaded areas are levels of hearing impairment. O **– right ear;** X **– left ear.**

3.3.2. **Visual-auditory Calibration**

Two types of calibration were completed for both visual and auditory stimuli: signal amplitude and temporal occurrence. In the case of the visual stimuli, measuring its amplitude meant determining the brightness of the cue, the fixation dot, as well as the brightness of the computer monitor when displaying a black image. These were

measures of luminance (cd/m^2) and were taken with a Gossen Mavo-Spot 2 high precision luminance meter, hand-held at the level of the participant's eye. In the case of the auditory targets, amplitude calibrations involved measuring the sound pressure level (dB SPL) with a Brüel and Kjær sound level meter type 2235. The sound was first measured in front of each speaker to check the pressure levels of both speakers (here a gain adjustment of 1.75 dB SPL was applied to the right channel to balance the speakers) and then calibrations were performed at the level of the participant's ear to ensure the sound delivery at the participant's ear was ~70 dBSPL. The other type of calibration aimed at checking the temporal relationship between the visual and auditory pair, since it is common for a computer with an operating system to introduce latency at several levels. Moreover, it was also necessary to check if the generated stimuli by the computer had the desired duration. This was accomplished using a digital phosphor oscilloscope (Tektronix DPO 4034) that received inputs from the left and right channels of the sound card and a colorimeter (ColorCal MKII; Cambridge Research Systems). The colorimeter's primarily function is gamma calibration of computer monitors, however, this particular device had a simple and very useful feature that allowed for the visual-auditory temporal calibration: when it detected a contrast change, a trigger was sent (figure 3-5). The colorimeter was then connected to the oscilloscope via an external link.

Auditory and visual stimuli were played consecutively every second for 1 minute and measured in the oscilloscope. A fixed delay of 100 ms was applied to all auditory stimuli to correct for the measured delay of the visual events.

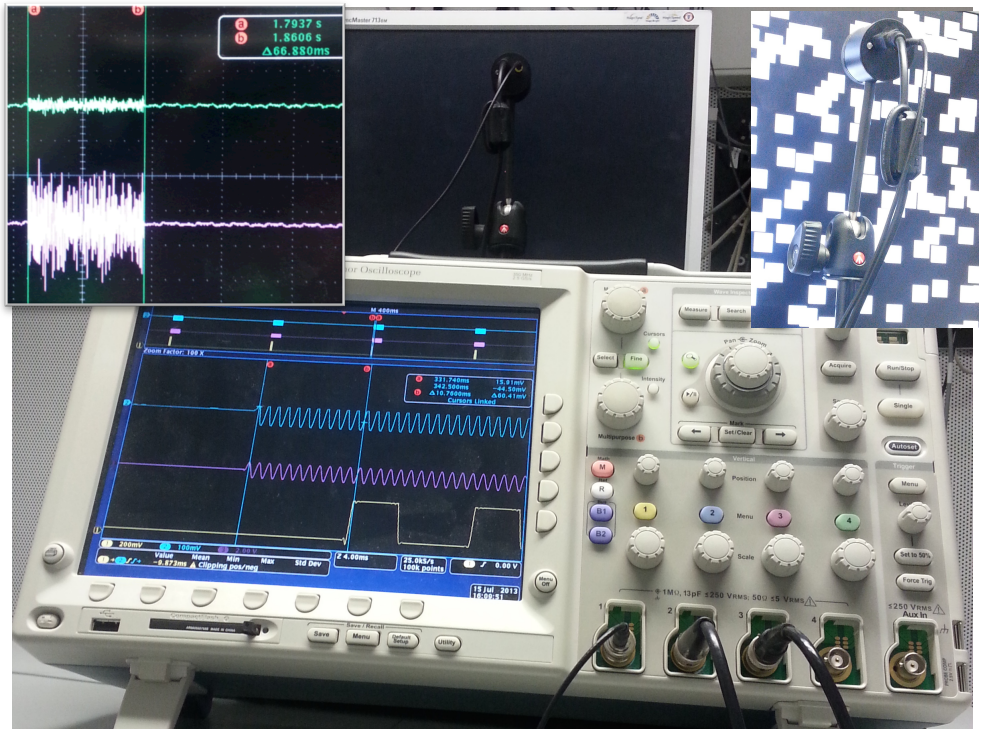

Figure 3-5 Temporal calibration set-up for the visual-auditory pairing. Blue and pink lines in the oscilloscope's screen are the left and right channel outputs of the computer's sound card, respectively. The yellow line is the pulse trigger from the colorimeter. The vertical blue lines are measuring the latency between the onset of the sound and the onset of the visual stimulus (100ms). Top left is an example of an auditory target's duration being measured (67 ms). Top right, the colorimeter calibrating the masking squares used in experiments 4 and 5.

Visual cues were 33 ms in duration and auditory targets were 67 ms (example of auditory targets on top left of figure 3-5), thus no further adjustments were required. ISIs between cue and target were also measured, but since a fixed delay had been applied to the auditory stimulus, no further adjustments were required.

Any variability observed in the measurement of the inter stimuli intervals (ISIs), and also in the duration of the stimuli, was in the order of decimals places, thus, it was assumed that this would not be sufficient to carry any perceptual consequences. Furthermore, this variability was attributed to manual placing of the oscilloscope anchor points (by the scientist) that determined the onset and offset of the stimuli. Figure 3-6 depicts the onset and offset anchors that are manually places to measure the duration of the stimuli.

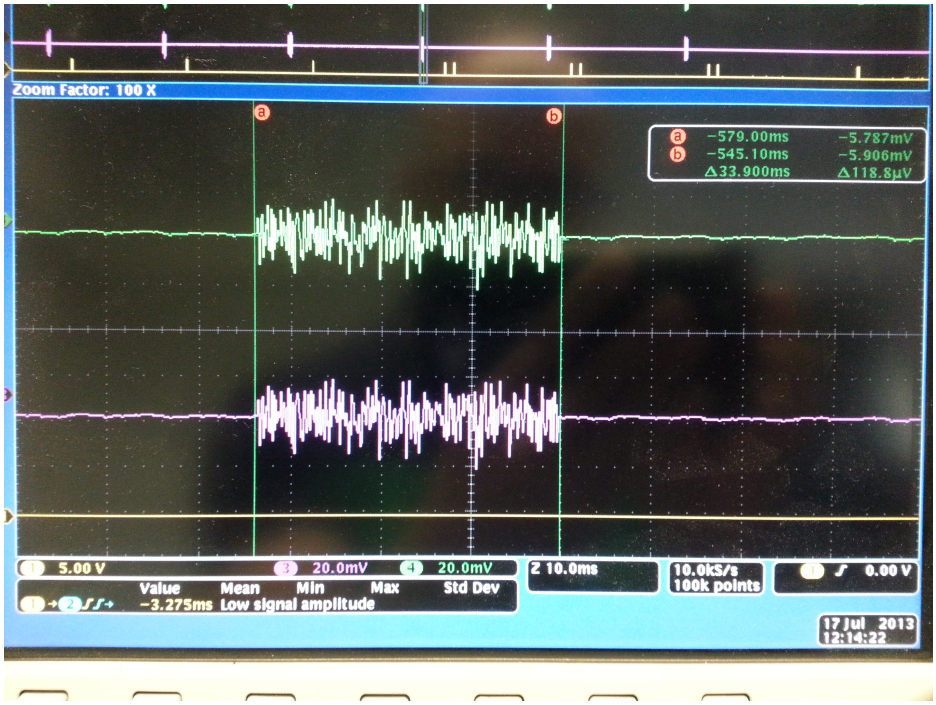

Figure 3-6 Measurement of auditory cue. Digital onset (a) and offset (b) anchors are placed manually to read the duration of the stimuli.

3.3.3. **Stimuli**

When referring to a pair of stimuli, by convention, the first modality in the pair is the cue and the second modality the target. So, for instance, when referring to VA pairing, this meant that the participant was presented with a visual cue and an auditory target. This convention will be maintained, throughout this thesis, for cross-modal and uni-modal conditions (AA, for example, is auditory cue and auditory target). In what follows, the physical attributes of the visual and auditory cues and targets for experiments 2 to 6 are described. The calculations used to display the visual stimuli on the computer screen are discussed next. The duration of the visual and auditory stimuli were computed as multipliers of the monitor's refresh rate (16.7 ms for a 60Hz monitor).

3.3.3.1. *Central fixation dot*

The central fixation dot was 0.2° diameter with a luminance of 2.80 cd/m^2 (measured with a Gossen Mavo-Spot 2 high precision luminance meter).

3.3.3.2. *Auditory cue*

The auditory cue was a 33 ms duration broad band noise (BBN; 3 ms cos^2 ramp) between 200 Hz and 1200 Hz, band pass filtered with a 6th order Butterworth filter, measuring ~70 dBSPL at the centre of the chin rest (Brüel and Kjær sound level meter type 2235).

3.3.3.3. *Visual cue*

The visual cue was a white circle (4.27 cd/m^2) lasting 33 ms with a radius of 0.75° and a vertical position of 6.4° above the centre dot. The horizontal position of the visual cue was drawn randomly every trial from one of three locations: middle (centred at 0°) right and left (±10°).

3.3.3.4. *Auditory target*

Auditory target was a 67 ms BBN band passed with a Butterworth filter with a low cut-off frequency of 200 Hz and a high cut-off of 1200 Hz. A 3 ms onset/offset cos^2 ramp was applied to all auditory stimuli to prevent onset and offset distortions (clicks) when playing the stimuli. Auditory targets appeared in one of seven locations linearly spaced; three positions to the left of the fixation dot (-7.5°, -5° and -2.5°), one in the centre (0°) and three positions to the right of the fixation point (2.5°, 5° and 7.5°). The speakers were positioned 6.4° above the centre of the screen (see figure 2-1). The location of the auditory targets was accomplished by using a linear amplitude panning. The pan position value was computed between 0 and 1, with 0 representing hard left (or 32.8°, which corresponds to the position of the left speaker), and 1

representing hard right. The relationship between pan value and perceived lateral position was not directly validated, thus, specification of auditory sound source locations in degrees should be considered only approximate.

3.3.3.5. Visual target

The visual targets were two vertical aligned lines (vernier; 1.7° long; 0.1° wide) centred 5.55° above and below the fixation dot, with a luminance of 10.38 cd/m^2. The duration of the visual targets (vernier lines) was 67 ms. Visual target stimuli appeared in seven locations (linearly spaced); three to left of the bottom line (-0.6°, -0.4° and -0.2°), one directly above the bottom line (0°) and three locations to the right of the bottom line (0.2°, 0.4° and 0.6°).

3.3.3.6. Visual Masking squares

Preceding the participants' response in experiments containing a visual target (AV and VV), 250 visual masking squares (2° edge length; 13.7 cd/m^2) were randomly drawn for 250ms, in order to disrupt the visual afterimages created by the vernier target.

3.3.4. **Calculations to display objects on a computer screen**

The experiments were coded in Matlab (MATLAB 7.9, The MathWorks Inc., Natick, MA, 2000), using the Psychophysics Toolbox Version 3 (PTB-3) extension (Brainard 1997; Pelli 1997). To code objects on screen, instructions have to be given in units of pixel. To explain how visual stimuli were displayed let us consider a practical example of displaying an open circle. The calculations shown here are generic and were also be adapted to display the masking squares and vernier lines.

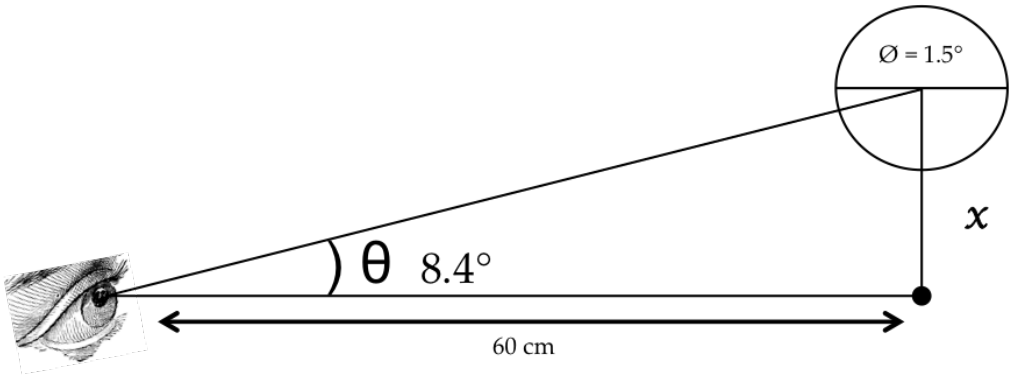

Figure 3-7 A circle with 1.5° of diameter is displayed 8.4° above the fixation dot.

To display a circle with a 1.5° of diameter at 8.4° above the fixation dot (figure 3-6), we first need to establish the participant's distance to the computer screen. If the participant is 60 cm from the screen, we can easily calculate the distance from the fixation dot to the center of the circle, denoted by the *incognita* x, by applying the fundamental notions of trigonometry. Since the screen is perpendicular to the horizontal plane of view (in parallel to the floor), we want to calculate the length of the opposite side (in relation to the eye) in a virtual right-angle triangle. Since we know θ (theta) to be 8.4°, and the adjacent side to be 60 cm, we can use the tangent formula:

$$\tan 8.4 = \frac{x}{60\ cm}$$

, which gives x = 8.86 cm.

Since the distance from the centre of the circle to the fixation dot is 8.86 cm, we need to know how many pixels that distance translates to. Let us consider that our computer screen is 1280 by 1024 resolution, 376.3 mm wide, 301 mm tall of pixel area (without plastic bezel). In other words, there are 1280 pixels in 37.63 cm of display area of the screen (or 1024 in 30 cm). This means that there are 34 pixels per 1 cm of display, and, therefore, (8.86*34) 301.24 pixels from the fixation dot to the centre of the circle. The fixation dot will always serve as an anchor from which

to display graphics on screen since it can be easily calculated by diving both resolution measures by 2: 1280/2 = 640 (pixels from left or right) and 1024/2 = 512 (from top or bottom). Since the radius of the circle is 0.75°, we can apply the same calculations replacing θ with (8.4° - 0.75°) 7.65°. We shall call this angle α. By doing this we can calculate the distance from the fixation dot to the bottom of the circle: tan (7.65) × 60 cm $= x \Leftrightarrow x = 8.06$. Figure 3-7 shows the spatial relationship between objects on screen. Multiplying this result with 34 (number of pixels in 1 cm) gives us the amount of pixels from the centre of the screen to the bottom of the circle: 274 pixels.

The radius can now be calculated: 301,24 (pixels from centre of screen to centre of circle) – 274 = 27.24 pixels. With the radius we can now calculate the diameter in pixels (27.24 × 2 = 54.48) and the position of the top of the circle (301.24 + 27.24 = 328.48). The coordinates can now be coded in pixels, from the centre of the screen.

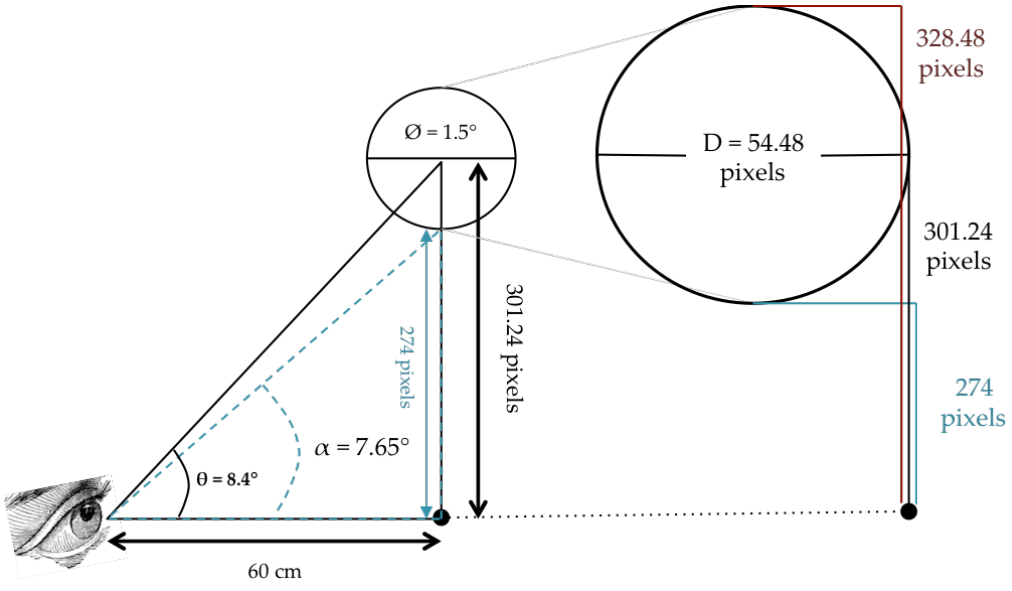

Figure 3-8 Spatial arrangement of circle coordinates in pixels from the centre of the screen, illustrated here as a black circle.

3.3.5. **General Data Analysis**

In order to perform statistical analysis to the behavioural data collected in the psychophysical experiments, a non-linear regression model was applied to all data sets. The aim of fitting a statistical model to a given set of observations is to benefit from the possibility of extrapolating unobserved values. This is particularly useful since it is impractical and difficult to design an experiment that presents stimuli at the individuals' subjective thresholds (which might even be what the experiment aims to determine). By fitting a non-linear regression model I aim to quantify the relationship between subjective perceptions (e.g., proportion of right responses, proportion of perceived brightness, etc) and a physical characteristic of a given stimuli (e.g., contrast, gap length, etc). The present thesis relates, for example, percentage of right responses (dependent variable) and target position (independent variable).

3.3.5.1. Non-linear regression models (NLRM):

The typical use of a non-linear regression model (NLRM) determines one or more parameters that summarise the subject's behaviour. These parameters are subsequently analysed to form statistical inferences. Wichmann and Hill (2001a, 2001b) and Kingdom and Prins (2010) provide a very readable and comprehensive discussion on all aspects related to non-linear fitting, evaluation and interpretation. However, some fundamental concepts necessary to understand the work here presented will be explained in following paragraphs (specifically descriptions of the key components of the fitted function and its goodness-of-fit). Statistical modelling is outside of the scope of this thesis, thus the reader is guided to the above-mentioned publications for more information and/or fitting guidance.

Some of the most commonly used NLRM in psychophysics today are the *logistic*, *cumulative normal*, *weibull* and the *hyperbolic secant* functions (Klein 2001; Wichmann and Hill 2001a; Kingdom and Prins 2010). It is important that the applied statistical model fits the data well in order for the predicted function to be as close as possible to true observations. Even though the aim of the present thesis is not to study different methods of non-linear modelling, the above four NLRMs were fitted to data from three random pilot participants (equations for these functions can be found in appendix 3.2) in order to understand which function should be used in our data. To illustrate this, figure 3-8 shows data from a representative pilot participant fitted with the four NLRMs (auditory target and auditory cue condition at 167ms).

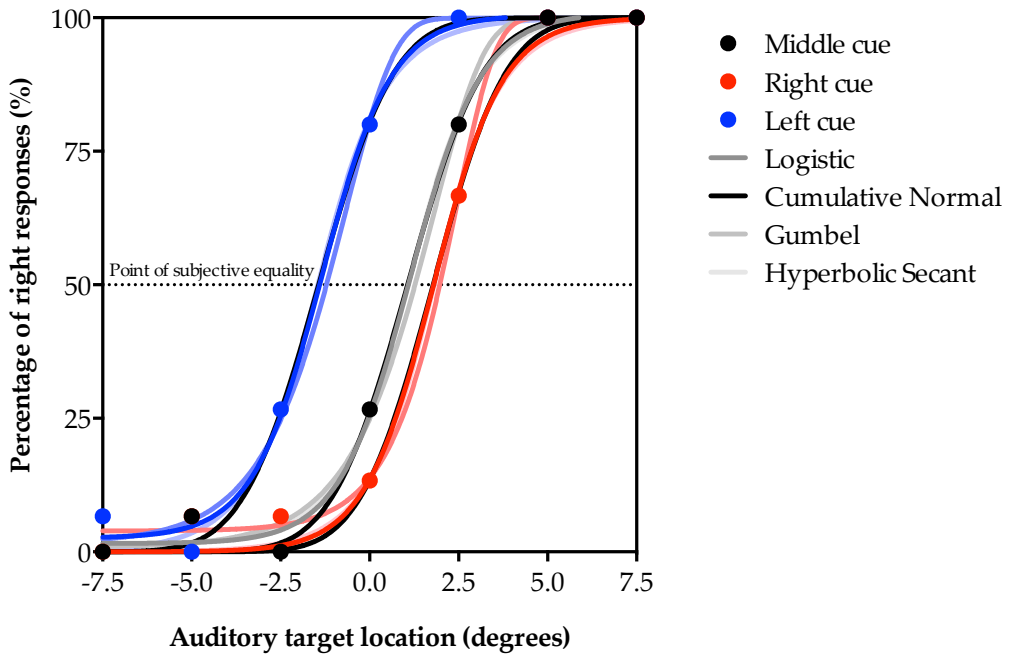

Figure 3-9 Representative data fitted with a Logistic, Cumulative Normal, Gumbel (log of Weibull) and a Hyperbolic Secant function. The three data sets (blue, black and red) correspond to the auditory cue position at the left (blue) middle (black) and right (red). Each data point corresponds to the location of the auditory target (7 locations). Dashed line is the PSE (point of subjective equality).

This figure will help introduce the fundamental concepts of psychometric behavioural analysis. Immediately it becomes obvious that the participant's performance differs according to the experimental

conditions. Data points in blue represent cueing arriving from the left and the participant's responses contrast (mainly in the abscissa position of the curve) for cues coming from the middle (black lines) and from the right (red lines). This difference is a measure of the bias induced by the physical stimuli and is reflected in the participant's behaviour and thus in the fitted functions. All functions have a sigmoidal shape and, as can be seen, the estimates of where the x-axis intercepts the 50% performance (in the y-axis) are very close for all four functions, regardless of cue position. The point in the abscissa that corresponds to 50% in the ordinates is called the *point of subjective equality* (PSE). The PSEs are depicted in figure 3-9 in more detail. In the present thesis, the PSE is where the participant is equally likely to respond that the target came from the left or from the right. All predicted PSEs are near identical (with a slight deviation for the Gumbel function).

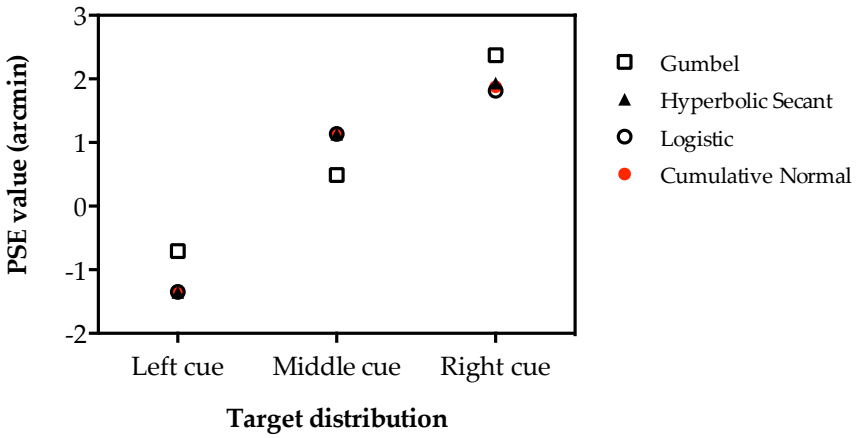

Figure 3-10 Point of Subjective equality (PSE) values for a representative pilot data estimated from the four psychometric functions.

This is a crucial aspect of the NLRM fitting: the determination of a *PSE*. Another important feature of NLRMs is the quantification of *discrimination*. Discrimination is described as the ability of our senses to distinguish a moving car from a faster moving car, or water from saltier water, for example. In the context of this thesis, discrimination is the

ability of the participant to distinguish a left from a right target. Thus, harder experiments are associated with shallower slopes and worse discrimination (or sensitivity). Both PSE and discrimination threshold are given by a function parameter, described below, which will be used later to perform statistical analysis. Finally, judging the above fits solely by looking at the depicted lines it is clear that all lines draw very close or on top of the data points, which indicates that all models can reliably be used to model the data. This brings us to another important aspect of psychometric fitting, the assessment of goodness of fit of the statistical model. A coefficient of determination (R^2) is commonly used to assess the *goodness-of-fit* (GOF) of psychometric models. R^2 values range from 0 to 1, with 1 indicating a perfect fit. Indeed, when looking at the goodness of fit of the above functions, all possess a coefficient of determination of 0.9 or higher. A more detailed description of the GOF used in this thesis will be described next, but to summarise, two important concepts were introduced here: the function parameters that determine the shape of the curve and form the independent attributes of the non-linear model, and the assessment of the goodness of fit or our model. These are vital aspects of the NLRM that will constitute the basis upon which statistical testing will be performed.

Since all functions did not deviate significantly from one another the *cumulative normal function* was chosen due to its simplicity (two parameter function; α and β), and a consistently robust fit across all data sets. Furthermore, the cumulative normal distribution is regularly used in psychophysical experiments to determine PSEs, in the same manner as in the present thesis (Lu et al. 2009; Watson and Krekelberg 2009; Spence and Parise 2010). This function was defined as follows:

$$100\times\left(\frac{1+\mathrm{erf}\left(\frac{x-\alpha}{\sqrt[2]{2}\times\beta}\right)}{2}\right)$$

erf being the Gauss error function, and α and β the two independent attributes of the function that correspond respectively to PSE (or mean of the function) and slope (or standard deviation of the function). In fact, this is a key property of the cumulative normal function: α is equal to the stimulus value corresponding to 50% right responses (the PSE), where the observer is equally likely to respond with either alternatives (in this case, left or right). This makes this function straightforward to interpret since the mean and standard deviation of this function are the indices of subjective performance and discrimination. Varying the α to positive or negative values will change the PSE to higher or lower values, respectively. On the other hand, varying the β will impact the slope of the curve. This is illustrated below in figure 3-10. The predicted α will be a direct measure of the participant's bias (or PSE) and is, therefore, the aim of psychometric fitting in the present thesis.

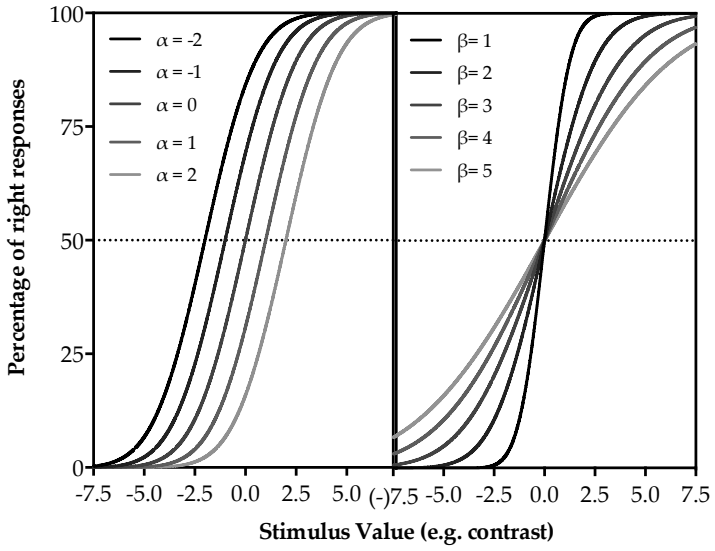

Figure 3-11 Cumulative normal psychometric function under different conditions of α and β parameters, which determine the shape of the fitted curve.

3.3.5.2. Determining the goodness-of-fit:

A necessary step in psychometric analysis is determining how well the observed outcomes are predicted by our statistical model (Wichmann and Hill 2001a) since a bad fit will invariably decrease the validity of predicted values. The coefficient of determination (R^2) was used to evaluate the goodness-of-fit (GOF) of our model. The R^2 determines how much of the variation in the subjective perception (e.g., percentage of right responses) is explain by the variation in the physical stimulus (e.g., location of the target). It compares the errors between observed and estimated outcomes:

$$R^2 = \frac{\sum_i (\hat{y}_{(i)} - \bar{y})^2}{\sum_i (y_{(i)} - \bar{y})^2}$$

where, $y_{(i)}$ is the ordinate integer of the data point; $\hat{y}_{(i)}$ is the ordinate predicted by the fitted NLRM; and $\bar{y}$ is the mean of the observed values. The R^2 varies between 0 and 1, with values close to 1 if the data points fall along the fitted PF, and close to 0 if they fall away from the fitted line. An R^2 of 1 indicates that data points fall precisely along the PF. Scores of 0.8 and higher indicate a strong fit with 80% (and higher) of the variation in the subject's performance being explained by variation in the physical variable. This means that only 20% of the variation in the subject's performance is not accounted by our model. The GOF will be used as an exclusion criterion whereby fitted functions with R^2 lower than 0.7 will not be included in further statistical analysis. This criterion will be one of three criteria used to ensure that the predicted PSEs are as close as possible to a true observation. The remaining criteria are explained below.

3.3.5.3. Exclusion Criteria:

In order to facilitate the understanding of the exclusion criteria, let us consider real data scenarios of excluded cases. For now focus should be directed to the contents of the graphics and not its axis (a more detailed explanation of the axis will be given with the first pilot experiment of the next chapter (*section 4.4.2*). In other words, focus should be directed to the data points, the fitted lines and how these two pieces interact (are data points far or close to the fitted line? etc.) and also how these two pieces look (do data points reach 100% performance?; is the fitted line sigmoidal, straight, steep, shallow, etc.).

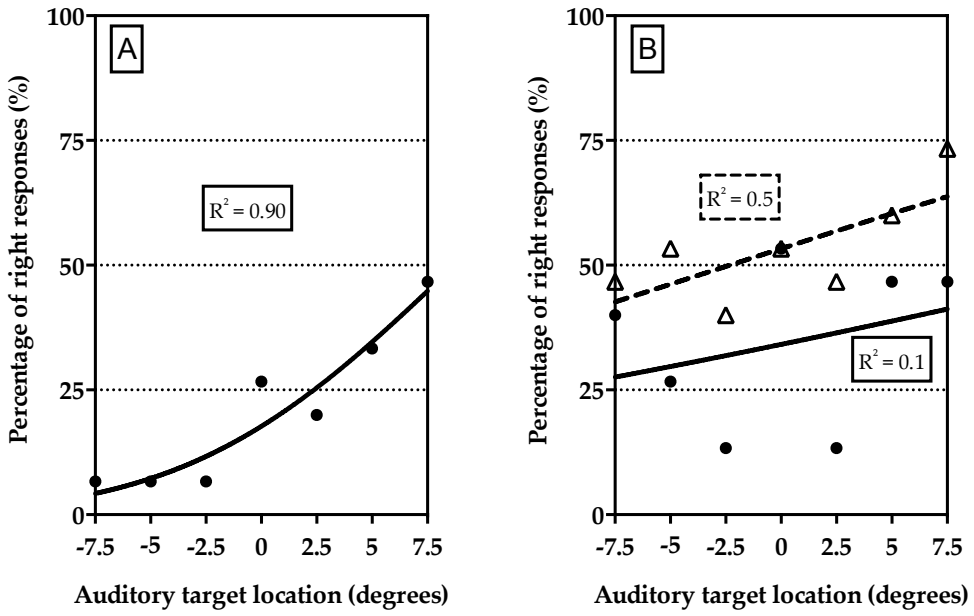

Figure 3-12 Exclusion criteria; A – example of unreliable PSE; B – Example of poor fitting.

There are *three exclusion criteria* that were applied to the data. Figure 3--12A illustrates an excluded data set based on the *first criterion*: the estimated point of subjective equality must rest between the possible physical range of targets (7.5° to left and right of centre for auditory targets and 0.6° for visual targets). In this case, the PSE is 8.7°, thus it is unreliable to take this point as a good estimate of this set's PSE (an

extended target range would be required to capture the full psychometric function).

The *second criterion* is illustrated in figure 3-11B: the coefficient of determination R^2 must be higher than 0.7, therefore indicating a good fit of the model. In this figure, both lines present a GOF that indicates a poor fit.

However, certain cases present a reasonable fit (R^2>0.7) and a credible PSE. This is the case depicted in Figure 3-12, where both data sets present a GOF of $R^2 > 0.7$, indicating that the NLRM fits well the data, and a physically plausible PSE (within the possible range of target stimuli).

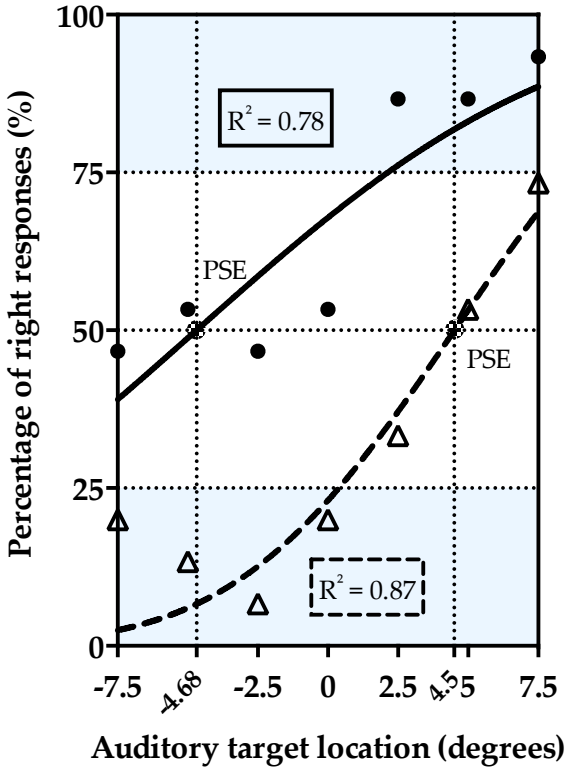

Figure 3-13 Excluded participant based on the third criterion. Solid line is condition visual cue, auditory targets; dashed line is auditory cue, auditory target condition. ↳ Denotes the point of subjective equality

But, these may not be accurate estimates of performance, since for instance, for the black solid fitted line, performance is near the chance

level (50% response). For these cases, a *third criterion* was implemented: the estimated model must reach at least 75% of responses at both extremes of the function (shaded portions of figure 3-12).

Taking for example the model with the solid line, it is clear that the task was too hard and despite reaching the 75% threshold to right targets, it did not reach the required 75% threshold to left targets. The data set fitted with a dashed line presents a performance that is the reverse, failing to meet the 75% threshold for right targets (function does not reach shaded top area). The three criteria have to be used interchangeably and/or in combination, whenever the case, for the exclusion to be logical and rigorous. For instance, in figure 3-11A, the GOF ($R^2 = 0.9$) indicates that this model represents accurately the data points and thus, the scientist can be confident in the predicted outcomes. However, the most extreme location of targets was 7.5° (to the left or right) which makes this point of subjective equality, which is beyond 7.5°, inaccurate. Moreover, the fact that the estimated model does not reach 75% performance to right targets is a further indicator that the task might have been too hard. If exclusion had been based on criterion 2 alone (the GOF), this set would have been erroneously included with high confidence (since the coefficient of determination R^2 shows a near-perfect fit).

3.3.5.4. Colour code for the plots

The colour code adopted in this thesis to represent the behavioural data from a spatial task is the following: blue for left cues, black for middle cues and red for right cues. An example of this can already be seen in figure 3-8, where several NLRM were fitted and coloured correspondingly. This code is useful to introduce the concepts of spatial attraction and repulsion: when a right cue induces a rightward shift of

the PSE, it is termed an attraction. The opposite (when a right cue induces a leftward shift of the PSE) is termed repulsion. The same is also true for left cues, with a repulsion being when a left cue induces a rightward shift of the PSE.

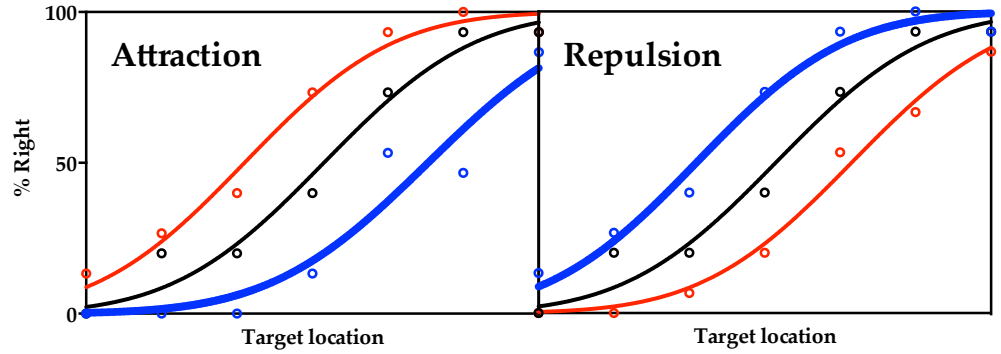

Figure 3-14 Examples of plots of attraction and repulsion of an auditory target that was preceded by a visual cue.

Since the participants' responses will always be plotted as percentage of right responses, a general rule of thumb can be applied throughout this thesis, illustrated in figure 3-13:

- A blue line to the right of black line is termed **attraction;**

- A blue line to the left of the black line is termed **repulsion;**

- A red line to the right of the black line is termed **repulsion;**

- A red line to the left of the black line is termed **attraction.**

2314567890

6443567290

9310987998

2095656820

1234620782

0164515678

3601905876

CHAPTER 4 VISUAL-AUDITORY (VA) ARE

4.1. EXPERIMENT 1

4.1.1. Introduction of experiment 1

As seen in the literature review of this thesis, abrupt sounds or flashes can draw attention to their location. Directing attention results in better spatial resolution (He et al. 1997), better accuracy (Eriksen and Collins 1969a; Colegate et al. 1973) and faster reaction times (Eriksen and James 1986; Posner and Petersen 1989). In this experiment I aim to investigate the crossmodal effects of visual attention on auditory spatial perception. Specifically I will investigate a novel experimental paradigm constructed from the classical ARE to test the attentional effects of a visual cue on auditory target localization. This paradigm will flash a circle at one of three locations (left, middle or right) followed by a sound. Participants will have to judge the sound and ignore the flash. Auditory spatial judgments that are influenced by a preceding visual event are not uncommon in the literature. In the spatial ventriloquism effect[21], an auditory event is perceived to originate from the same spatial location as a visual event. As these phenomena draw from the example of the illusion created by ventriloquists, whereby the speech produced by the ventriloquist appears to come from a puppet, the term ventriloquism has been applied, for decades, to cases of auditory spatial mislocalization due to a bias introduced by a visual distractor (Jackson 1953; Thurlow and Rosenthal 1976; Radeau and Bertelson 1977; 2005; Recanzone 2009). Several studies have replicated this illusion using bimodal stimuli that were relatively close to real-life events (a whisling kettle, Jackson 1953; a drummer and a

[21] A distinction is made from the temporal ventriloquism whereby an auditory stimulus dominates the percept of visual temporal rate (Stekelenburg and Vroomen, 2005).

voice reading a text, Radeau and Bertelson 1977), however, this effect is also found in unfamiliar events using very basic and meaningless stimuli. In fact, the majority of studies of the ventriloquism illusion used simple noise bursts or pure tones and light flashes or shapes (see Burr 2012). Although it is reasonable to consider that the stimuli used in the present paradigm are capable of creating such effect, it is important to clarify the fundamental notion of VA synchrony. Simultaneity between VA events is essential for the ventriloquism illusion (Bertelson et al. 2000; Bonath et al. 2007; Thorne and Debener 2008). Without this synchrony, the bimodal event would be perceived as two independent events. Introducing a delay between the visual and auditory events would be enough to disrupt the ventriloquism illusion, thus removing this illusion as a possible contributor to the effect.

Studies on auditory spatial discrimination that use a preceding visual cue to disrupt the perception of the auditory target traditionally report the ventriloquism effect as the reason for the observed attraction (see Stein 2012, for a review of the literature). In addition, the visual modality is known to dominate over the auditory modality in spatial tasks (while auditory dominates in temporal ones; Spence and Driver 1997). It is therefore plausible to accept that under visual-auditory asynchrony this pattern of attraction will be maintained and that the percept of the location of the sounds will be attracted toward the visual cue. However, attentional studies with crossmodal cues investigating visual influences on auditory spatial discrimination when the facilitatory cue is far from the foveated location are yet to be undertaken. In this experiment we investigate visual influences on auditory targets, when the attention to the visual cues is not the locus of interest (the location of the auditory target). Furthermore, the symmetry

of the attentional effects[22] has never been studied under this paradigm, thus I aim to investigate this by comparing left cue induced bias against right cue induced bias. Spatial bias is reported as being independent of cue side with the classical ARE paradigm (Suzuki and Cavanagh 1997; Pratt and Turk-Browne 2003; Pratt and Arnott 2008; Digiacomo 2013), thus it is expected that this trend is maintained here.

[22] Does attention to the left cue cause bigger bias than attention to the right cue?

4.1.2. **Methods of experiment 1**

In order to facilitate the understanding of the experiment I will begin by describing the data collection process as it unfolded from the perspective of the participant. This means detailing the experimental procedure first before describing the stimuli and the pilot experiments

4.1.2.1. Experimental Procedure

Participants were required to have normal hearing and normal (or corrected to normal) vision, to be included in this study. After completing a pure tone audiometry and completing the consent form, the participant was accompanied to a soundproof room. The participant sat in front of a computer screen with the head rested on a chinrest while maintaining gaze fixation on a dot displayed in the centre of the computer screen. The chair height was adjusted so that the participant's chin and forehead rested comfortably in the chinrest (figure 4-1 shows a photograph of the experimental set up, in the General Methods chapter). Participant instructions were as follow:

" When the experiment starts, there are three important events occurring. A flash, a sound and your response. These three events are sequential and constitute one trial. They will repeat themselves over and over until we reach the total number of trials. All you have to do is respond if the sound came from the left or the right. You will answer by pressing the buttons in the response box. Now, let's look at the events in detail (pointing to a printed card, also depicted in figure 3-1). You will first be presented with a dot at the centre of the screen. Please fixate on the dot for the entire trial and do not look elsewhere in the screen. This dot will remain on the screen for the whole session. Nothing will happen for a brief moment, except this dot. This marks the beginning of each trial. Then, after the dot, a white circle will flash for a very brief

moment at one of three locations, either at the right, at the middle or at the left. The location of the flash is random each trial, so I don't know where the circle will come from. Please ignore the flash and do not deviate your eyes from the centre of the screen. You will be able to see the flash with your peripheral vision. After the flash you will hear a brief sound coming either from the left or from the right. Please press the right red button if you think the sound came from the right, or the left green button if you think the sound came from the left. There will be times when it is very obvious that the sound came either from the left or from the right, and there will be times when it will be harder as the sound is closer to the centre. Other times, the sound will appear to have come from the middle. When you are not sure just press the button where you think the sound came from, or guess, and don't worry too much. Just make sure that if it is really obvious for you that the sound came from the left or right, you press the corresponding button. After you pressed the button, a new trial begins."

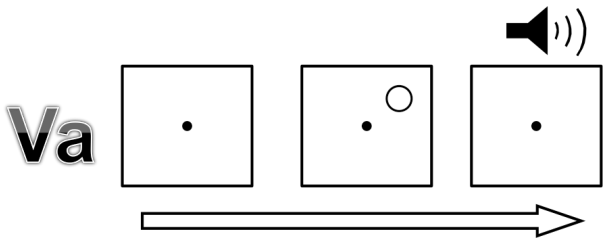

Figure 4-1 Card used to aid instructions to participants on the visual-auditory pairing events in experiment 1.

In the first session, participants were informed that the visual-auditory pairing (VA) was presented with a specific inter-stimulus interval (ISI), and that they were required to complete four sessions, each session corresponding to a different ISI between visual and auditory stimuli: 100ms, 500ms, 1000ms and 1500ms. The first stimulus in the pairing (visual) corresponded to the cue and the later (auditory) to the target. Each session lasted approximately 20 to 40 minutes (depending on the

response speed of the participant, instructions, and ISI) and the order of the sessions (which corresponded to an ISI) was randomised for each participant. Figure 4-2 shows a diagram of all the events in one trial. Due to the difficulty of the task, but to limit the effects of training, participants were allowed a maximum of one practice run comprising of two trials per target location, or until the tester was confident the participant understood the instructions. After practising the task, the lights were turned off and the eye tracker was calibrated. Participants were instructed that after calibration of the eye tracker they could not move their head until the experiment was over. Each participant completed a block of 315 trials (15 repeats of 7 target locations and 3 cue locations). During each trial, the location of the cue and target stimuli was randomized.

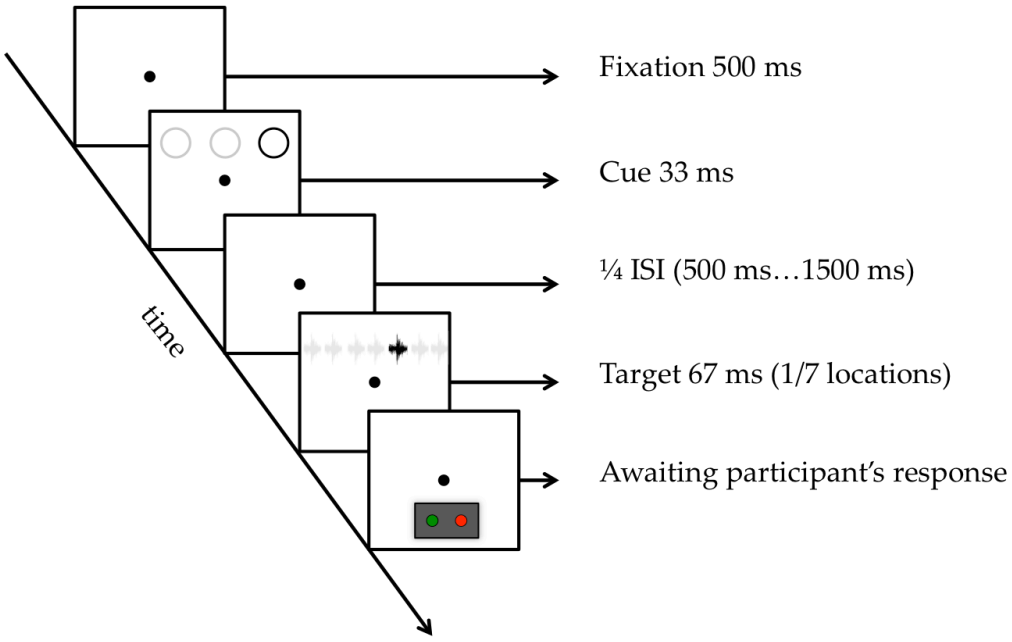

Figure 4-2 Sequence of events during one trial of experiment 1. VA pairing consisted of a visual circle presented either in the left, right or centre, and an auditory target presented in one of seven locations. Participants completed 4 different inter-stimulus intervals (ISI), with each ISI comprising 315 trials of 15 repeats per cue per target (15x3x7).

4.1.2.2. Stimuli

Stimuli consisted of a visual cue and an auditory target. The details of the VA stimuli pairing used in this experiment as well as the respective

calibration procedures can be found in the General Methods chapter (3). Succinctly, the auditory target (66 ms duration) consisted of a short BBN (66 ms of duration) randomly presented each trial at six locations equidistant to the midline (0°). The visual cue (33 ms duration) was a circle randomly displayed at three locations, each trial: left, right and centre (Illustrated in figure 4-3). Four interstimulus intervals (ISI) were tested: 100 ms 500 ms 1000ms and 1500 ms.

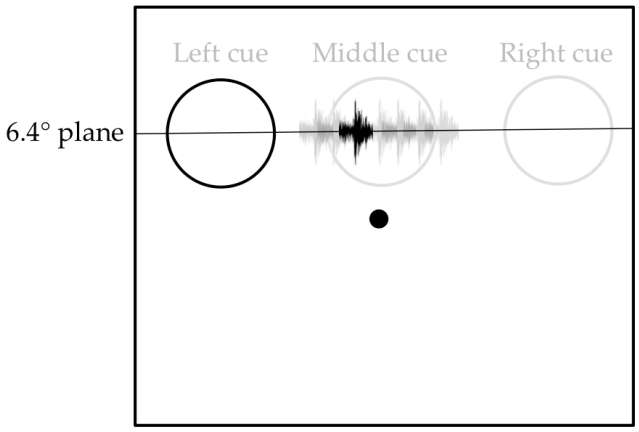

Figure 4-3 Relative positions of cue and targets as seen by the participant with reference to the 6.4° plane, where the centre of the speaker cones were positioned.

4.1.2.3. Pilot experiment

An important step in psychophysical experiments is the determination of the step size or interval range of the independent variable, by convention in the abscissae axis. In our case, this refers to the locations of the auditory target stimuli. If targets were too close together (and since they are always equidistant to the centre) the task would be too difficult (meaning that participants would not be able to distinguish a left sound from a right sound as it would always appear to have come from the middle). In that case, the fitted non-linear regression model (NLRM) would indicate that performance would not significantly rise above chance level. Ideally, in an optimal 2-alternative-forced-choice psychophysical experiment, the physical stimuli should use values where performance is just below 100% (Kingdom and Prins 2010). In

order to determine the locations of the auditory targets, seven linearly spaced auditory targets were first created and presented to three auditory scientists (including the author of this thesis) in a manner similar to the procedure aforementioned in this section (*4.1.2*), using only the ISI 100ms. The auditory targets selected for this small test were notably spread apart: -15°, -10°, -5°, 0°, 5°, 10° and 15° (three targets to the left of the midline and three to the right). The aim of this pilot was to investigate if an informed participant could easily detect this targets, so a steep function was expected (with perhaps some floor and ceiling effects). Feedback was gathered and the chosen NLRM was fitted. Data were plotted in a graphical format with figure 4-4 showing the NLRM's best-fitted line, according to the general data analysis methodology described in *section 3.3.5*.

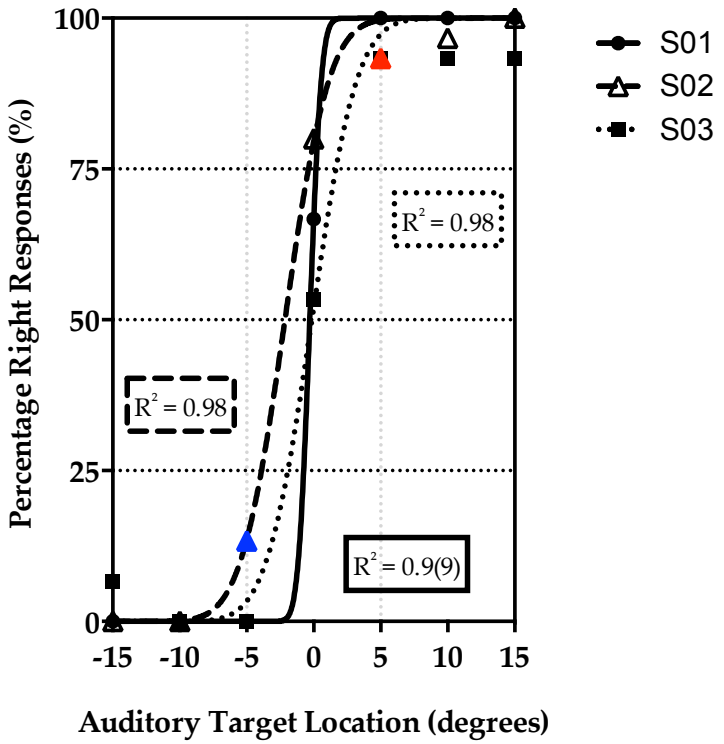

Figure 4-4 First pilot data collected for auditory targets ranging of -15° to 15°. Lines represent the best-fit non-linear regression model. S01/2/3 is participant 1/2/3.

In the above figure (4-4), only the responses to the middle cues are plotted because the responses to the left and right cues did not differ under visual inspection, thus for now, they would just clutter the plot. The abscissae show the location of the auditory targets (in degrees) and the ordinates show the percentage of right responses. The red and blue data points will be used to explain the plot further: the red data point illustrates the average response of participant 2 to the 15 trials of the target located at 5° to the right. The remaining data points are also averages of the 15 trials, with each point corresponding to a specific target location (in degrees). The average response for this target (red triangle) was 93 % of right responses. In other words, the participant responded RIGHT 93% of the times this target was presented. Since this target was presented 5° to the right, the participant was accurate in responding "right".

Conversely, this is the same as saying that 7% of the times, the participant answered: "left". If for instance we take the blue triangle, we can see that this data point refers to the target presented 5° to the left. The average of responses here is 13.33% to the right. As before, this is the same as saying that the participant responded LEFT 86.67% of the times this target (a left target) was presented (in this case 5° to the left). It is important to look at the graphic both ways because the 75% performance for right responses is depicted in the 75% horizontal dashed line (in the y-axis), but the 75% performance of left responses is depicted in the 25% horizontal dashed line. In other words, and since all graphics will be plotted as a percentage of right responses, if we want to look at the 75% performance of left responses, this can only be done by looking at the 25% performance line. In sum, going back to the results, this participant detects very well the targets presented at 5° in

space, regardless if these come from the left or from the right. Accordingly, both functions show a steep curve, which is indicative that the participant show a good discrimination of the targets. Furthermore, several data points reach the maximum performance at both sides of the function (0% and 100%), which may not be ideal in a psychophysical experiment (too many trials have been wasted presenting stimuli that was too easy). Based on this, the task was made more difficult with a second pilot, since the aim was to "zoom in" on the PSE (at 50% performance).

Three naïve participants (students from the University of Nottingham) with normal hearing (as confirmed by a PTA) and normal vision, participated in the second pilot experiment aimed at testing the protocol, set up and the new target locations. The updated target locations were seven locations, linearly spaced: three to the left and right of the centre (-7.5°, -5°, -2.5°, 0°, 2.5°, 5° and 7.5°). The reason for choosing to reduce the step size of target locations by only 2.5° was because the two participants above were very good at spatial discrimination tasks, which means that reducing the step size further could make the task too difficult for naïve participants. Data was collected according to the procedure illustrated in figure 3-2 (using only the ISI of 100 ms). Figure 3-5 shows a representative participant of the second pilot. Red data points and line represent the responses to trials containing a right visual cue. In the same way, black represents responses to trials containing a middle visual cue and blue represents responses to trials containing left cues.

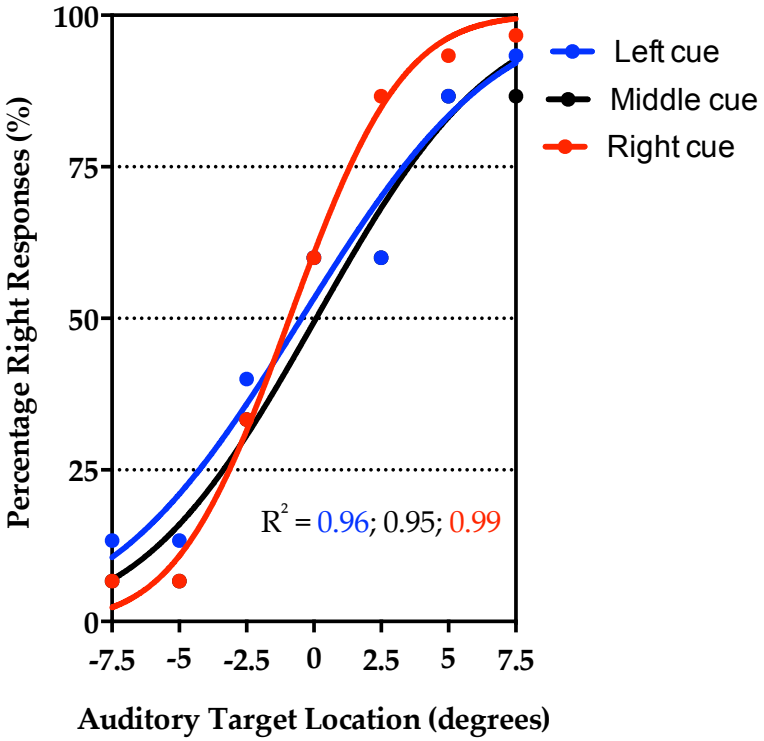

Figure 4-5 Representative participant of second pilot of experiment 1. Auditory targets ranged from 7.5° to left and right of middle line. Blue, black and red colours indicate cues coming from the left, middle and right, respectively.

Examining the above figure (3-5) and taking into account the exclusion criteria described in *section 2.3.3*, it can be concluded that the NLRM fits well the data, with a GOF R^2 above 0.95 for all cue positions (left, middle and right). Furthermore, PSEs (point of subjective equality) are plausible (within the physical range of presented targets) and all three curves reach the 75% performance, without prominent ceiling or floor effects. This is indicative that the range of targets was appropriate for naïve participants. In summary, the three participants showed good R^2 values for all cue positions, as well as performance above the 75% and plausible PSEs. Feedback was gathered regarding the comfort of the set-up, brightness of cues, loudness of sounds, ease of understanding of the instructions and difficulty of the task.

4.1.2.4. Participants

A total of 10 participants (4 males), with age ranging from 19 to 32 years (mean of 23.61, mode of 22) took part in experiment 1. No participants were excluded after applying the rejection criteria to the data (detailed in the general data analysis section, chapter 2). To succinctly repeat the rejection criteria, there were three: one, the estimated PSE must be within the physical range of target values; two, the coefficient of determination (R^2) that evaluated the GOF of the model must be higher than 0.7; and three, the estimated model must reach 75% performance. Participants were naïve to the purpose of the study and had normal hearing, confirmed by a five-frequency pure tone audiometry and normal vision.

4.1.3. **Results of experiment 1**

The points of subjective equality were calculated according to the general data analysis procedures in *section 3.3.5* of the General Methods chapter. Illustrated in figure 4-6 is the NLRM fitted to data of a representative participant at ISI 100 ms.

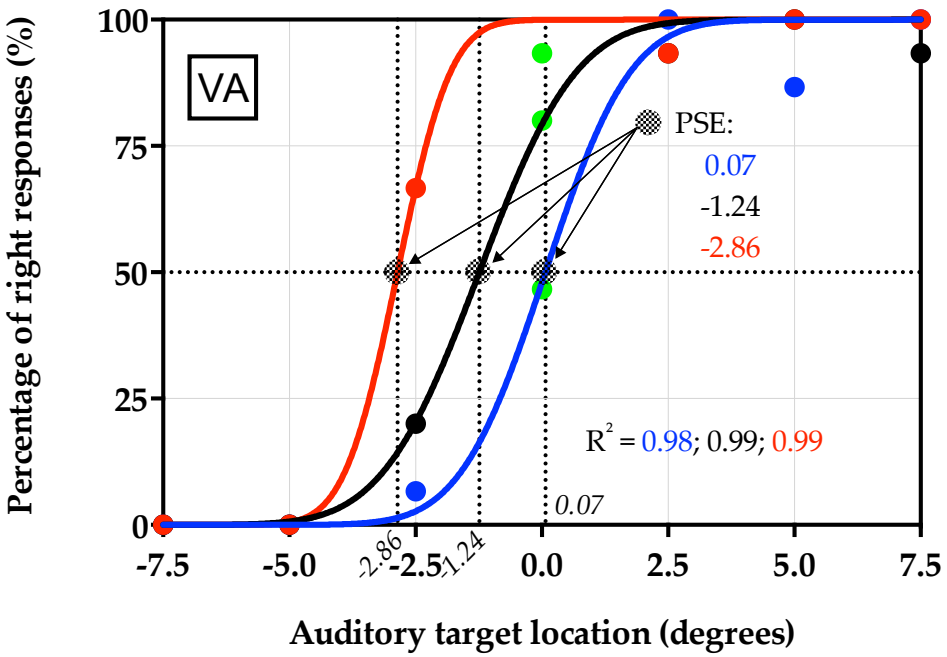

Figure 4-6 Data from representative participant illustrating the PSE and GOF. *Blue* represents visual cue in the left, *red* is visual cue in the right and *black* is visual cue in the centre. Green datum points are used in the text to explain the contents of the graphic.

Red colour indicates cues presented at the right, black at the center and blue at the left. The three green data points correspond to the following: the top datum are the proportion of right responses to the 15 trials (expressed as percentage) to a target presented at 0° (in the center), when a preceding visual cue was flashed at the RIGHT; the bottom datum are the average responses (to the 15 trials) to a target presented at the same location (0°), when a preceding visual cue was flashed at the LEFT. In the case of the top datum, when a cue arrived from the right, the participant responded RIGHT 93% of the times to the target in

the center. In the case of the bottom datum, when a cue arrived from the left the participant answered RIGHT 45% of the times to a target coming from the center. The middle green datum represents the average responses to cues and targets presented in the middle. Here, the participant responded RIGHT 80% of the times. Putting it all together, it can be seen that for this participant, middle and right visual cues have perceptual effects on the spatial detection of an auditory target. In other words, this participant presents a right bias when right and middle visual cues are presented before an auditory target. Furthermore, it can be said that left cues are neutral since they do not induce such bias (the participant responded RIGHT 45% of the times, and LEFT 55% of the times). The amount of perceptual shift induced by a left or right visual cue was calculated using the three PSEs. Left bias was defined as the PSE given by the left cue minus the PSE given by the middle cue. Similarly, right bias was defined by the PSE of the middle cue minus the PSE of the right cue. This notion is illustrated in figure 3--7. Results were transformed into minutes of arc (1 arcmin = 0.0166 degrees of arc) to allow better comparisons with the literature (see Suzuki and Cavanagh 1997; Pratt and Arnott 2008).

A repeated measure ANOVA with ISI (4 levels: 100, 500, 1000 and 1500 ms) and bias side (2 levels: left bias and right bias) as the within-subject factors was used to compare the main effects of stimuli ISI, cue side and their interaction on the spatial perception of naïve participants. The Mauchly's test statistic indicated that sphericity was violated for ISI therefore a Greenhouse-Geisser correction was applied. The bias side and the interaction did not violate the assumption of sphericity, therefore no corrections were applied. There was a main effect of ISI [$F(1.25, 11.26) = 8.124$, $p = 0.01$], however, there was no main effect of

bias side [F(1, 9) = 0.045, p = 0.84], and no significant interaction between ISI and bias side [F(3, 27) = 0.747, p = 0.53].

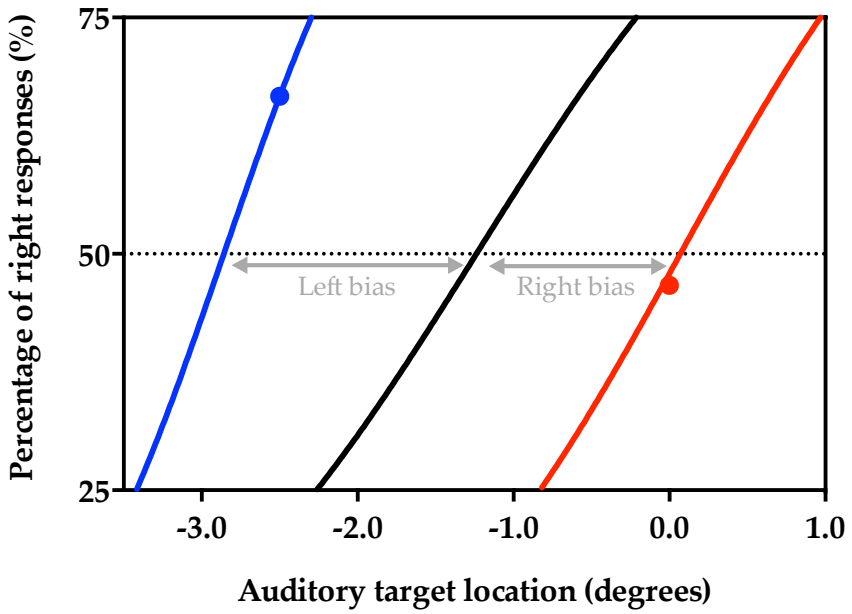

Figure 4-7 Example of bias calculations in a zoomed in portion of the PSE of a NLRM fitting. *Blue* represents visual cue in the left, *red* is visual cue in the right and *black* is visual cue in the centre. *Left Bias = Left PSE – Middle PSE; Right bias = Middle PSE – Right PSE.*

Since the size of the spatial bias did not differ with visual cue side, an average measure of bias was taken in an attempt to increase statistical power. This measure was defined as the mean of the bias induced by the left cue and the bias induced by the right cue. A new repeated measure ANOVA with only ISI as a factor (the same 4 levels) was used to investigate the effects of the different delays between cue and target on the spatial perception of an auditory target of naïve participants. A Greenhouse-Geisser correction was applied due to the violation of the assumption of sphericity given by the Mauchly's test of sphericity. There was a main effect of ISI at $\alpha < 0.05$, [F(1.35, 12.16) = 9.71, p = 0.006], which indicated that manipulations of the interval between cue and target significantly alter the spatial percept. Post-Hoc comparisons were performed to investigate in more detail how the spatial bias differed with ISI.

A paired samples t-test showed a significant difference between ISI 100 ms (M = 59.2; SE = 17.3) and ISI 1000 ms (M = 15.9; SE = 4.9), and between ISI 100 ms and ISI 1500 ms (M = 5.8; SE 4.8) p = 0.03. Bonferroni was used as the adjustment for multiple comparisons. Figure 4-8 shows the average bias across ISI. Looking at the figure, it becomes clear that the spatial attraction of auditory targets towards the location of visual cues decreases as a function of increasing ISIs. This notion was confirmed with a polynomial trend analysis, where planned contrasts demonstrated a significant linear decrease in spatial attraction [F(1,9) = 10.37, p = 0.01].

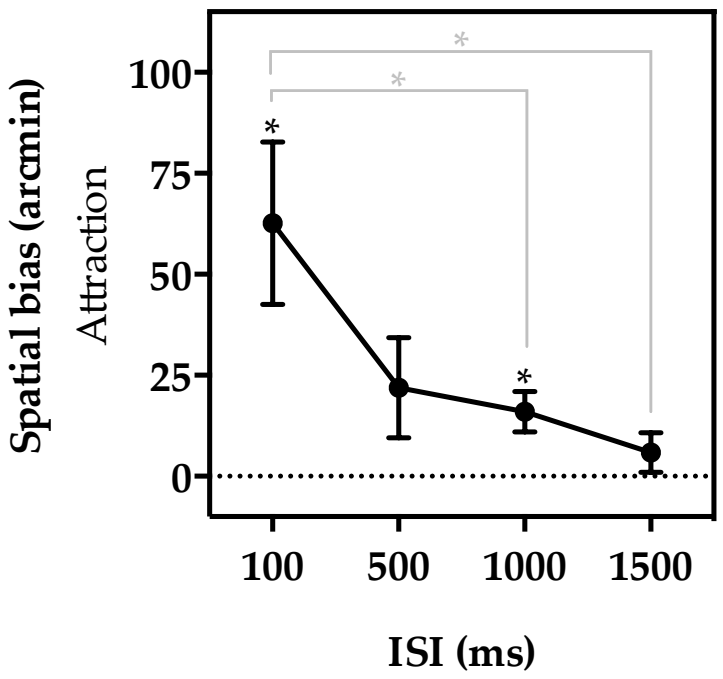

Figure 4-8 Average spatial bias across ISI. The bias induced by a visual cue on an auditory target decreases with the temporal interval between them. Asterisks represent a statistically significant difference. Error bars are SE.

A one-sample t-test was used to investigate if the observed attraction was significantly above zero in each ISI. Results were corrected using a Holm-Bonferroni adjustment. With this method the *p* values of the test statistic for *k* comparisons are sorted from the smallest to largest and compared to $\alpha/(k+i)$, with "*i*" being zero for the first comparison, and 1

minus the position that each *p* value occupies, for the remaining comparisons. In more detail, 4 comparisons were performed using a one-sample t-test with the following resulting *p* values (sorted from smallest to largest): 0.008 (ISI 100 ms), 0.011 (ISI 1000ms), 0.098 (ISI 500 ms), 0.258 (ISI 1500 ms). The first p value is then compared to 0.05/(4), the second to 0.05/(4-1), the third to 0.05/(4-2) and the forth is compared to 0.05/(4-3). Table 1 shows each ISI and the respective *p* value, and the adjusted alpha value used to correct for multiple comparisons. There was a significant difference between the spatial bias at ISI 100 ms (M = 59.2; SE =17.3) and the zero line (which refers to the absence of spatial bias), t(9) = 3.4, p = 0.008, suggesting a strong visual attraction of the auditory target. Additionally, ISI 1000 ms also shows a significant attraction t(9) = 3.2, p = 0.011.

ISI (ms)	*p* value	Adjusted alpha
100	0.008	0.013 *
500	0.098	0.025
1000	0.011	0.017 *
1500	0.258	0.05

Table 4-1 The ISI and respective *p* values were compared to an adjusted alpha using the Holm-Bonferroni correction. Asterisks mark the significantly different comparisons.

4.2. EXPERIMENT 2

4.2.1. Introduction of experiment 2

The previous experiment showed a consistent attraction across ISI and tended to zero as ISIs increased. It would be interesting to test the abovementioned effects when the ISI between cue and target approaches synchrony. The next experiment will look into attentional effects under very brief but asynchronous cue-target intervals.

The aim of experience 2 is to expand on the paradigm used in experiment 1, by looking at how auditory spatial perception would be influenced by visual cues when the ISI decreased from 500 ms to 16 ms. In the previous experiment we demonstrated that sounds can be attracted towards a preceding visual cue. It was established that this attraction was maximum at 100 ms, and tended to zero thereafter. The aim of the present experiment was to investigate this behaviour while ISI decreased in latency. In experiment 1, four ISI were tested (100, 500, 1000 and 1500 ms). Here we attempt to replicate two of the previous ISIs (in order to test the consistency of the effect), the 100 ms and the 500 ms and further test four more ISIs: 16, 50, 167 and 200 ms. This would allow for a fine sampling of the effect's time-course.

If the effect observed in the previous experiment is due to attentional effects, it would predict that the spatial bias would gradually increase until it peaks at around 200 ms and quickly declines at longer intervals (Colegate et al. 1973; above 300 ms, Eriksen and Hoffman 1973).

4.2.2. **Methods of experiment 2**

4.2.2.1. Experimental procedure and stimuli

The experimental procedure of experiment two is identical to the procedure described for the previous experiment, with the exception of the amount of ISIs tested. The present experiment tested the following ISIs: 16, 50, 100, 167, 200 and 500 ms. Each ISI was tested in a session, with the participant completing a total of 6 sessions. Each ISI comprised 315 trials of 15 repeats per cue per target (15x3x7).The VA pairing consisted in the same visual circle (presented either in the left right or centre) and the auditory target presented in one of seven locations (described in the general methods chapter, section; linearly spaced between -2.5° to 2.5°).

4.2.2.2. Participants

A total of 32 participants took part in experiment 2, however, 12 participants were excluded from further statistical analysis for meeting one or several exclusion criteria described in the General Methods section). Because the present experiment is a repeated measures design, exclusion in one or more ISIs meant that the entire data set for that participant would have to be excluded from the experiment. In other words, if for example data from participant S27 were excluded from the ISI 167ms, it would also have to be excluded from the remaining ISIs (16, 50, 100, 200, and 500 ms). This is a strict but vital aspect of the experimental design, aimed at preserving the internal validity of the experiment. Hence, data from 20 participants (8 males), with age ranging from 19 to 58 years (mean of 24.66, mode of 23) were selected for this study. Participants were naive to the purpose of the study and had normal hearing, confirmed by a five-frequency pure tone audiometry and normal, or corrected to normal, vision.

4.2.3. **Results of experiment 2**

The PSEs for each cue position in each ISI were calculated according to the procedure detailed in the General Methods chapter (3). Left and right bias were calculated[23] a factorial repeated measures analysis of variance was used to compare the main effects of ISI, bias side and their interaction on the spatial perception of naïve participants. ISI included 6 levels (16, 100, 167, 200, and 500ms) and bias side consisted of two levels (left and right bias). The Mauchly's test statistic indicates that sphericity was met for all conditions and interactions, therefore no corrections were applied to the data. The main effect of ISI, bias side and their interaction is reported as not significant and yielded an F ratio of $F(5, 95) = 1.138$, $p = 0.346$, for the ISI; $F(1, 19) = 0.562$, $p = 0.463$ for the bias side; and $F(5, 95) = 0.541$, $p = 0.745$ for the interaction.

Furthermore, pairwise comparisons of bias side and ISI did not yield any significant results, indicating that there is no difference in the induced spatial bias between the different conditions. Because there was no effect of bias side an average measure of bias was computed[24] to increase statistical power. This is also exemplified in figure 3-7. A one way repeated measures ANOVA was used to test the effect of ISI (6 levels) on spatial perception. The main effect of ISI (which met the sphericity assumptions) was reported as not significant $F(5, 95) = 1.138$, $p = 0.346$, indicating that the interstimulus interval had no main effect on spatial perception. This can be seen in figure 4-9, depicting the averaged bias across ISI, where the data points for each ISI lie near--horizontally in respect to each other. Additionally, pairwise

[23] **Left bias** = left PSE – middle PSE; **Right bias** = middle PSE – right PSE

[24] **Average bias** = (left bias + right bias)/2

comparisons show that none of the ISIs induced significantly different biases from one another.

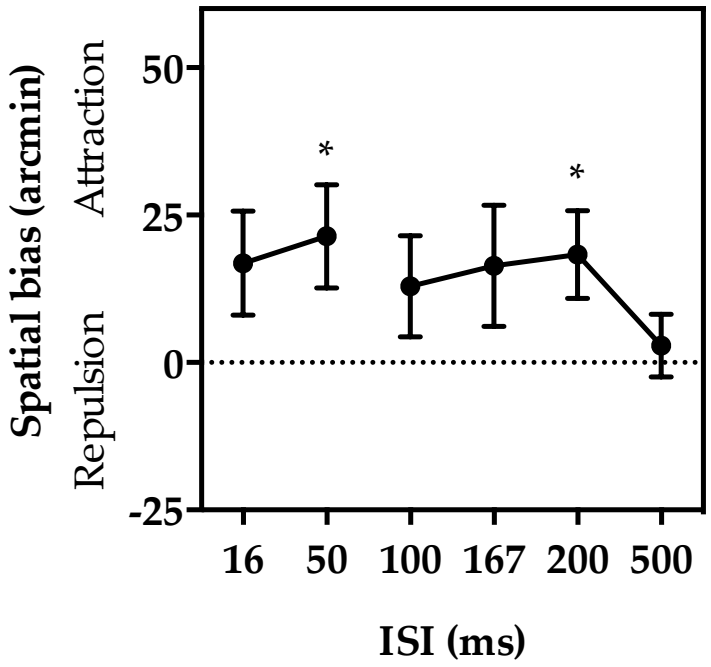

Figure 4-9 Averages of the visual bias of an auditory target are plotted across ISI. Error bars are SEM.

A one sample T-test was used to determine if the spatial perception induced by the visual cue is significantly above zero, or in other words, does a visual cue induce a statistically significant auditory bias? In figure 4-9 that shows the mean bias for each ISI it can be seen that all data points are above the zero line, which confirms an auditory attraction to the side of the visual cue. Because the one sample t-test strongly relies on the assumption of normality, a Shapiro-Wilk[25] test was used to examine to determine the extent to which the assumption of normality was met. This test is reported as non-significant, indicating that the data did not deviate from the assumption of normality. On average, the spatial bias induced by the visual cue did not differ

[25] The Shapiro-Wilk test was chosen for being more accurate and generally more appropriate for small samples (< 50 samples Field, 2009).

significantly from zero, regardless of the ISI, at a significance level of p = 0.0083, after Bonferroni correcting for multiple comparisons (means and standard deviations are shown in table 4-2). Despite this, ISI 50 ms and ISI 200 ms show an attraction that is significantly above zero before the stringent Bonferroni corrections were applied, t(19) = 2.45, p = 0.02. Since the size of the difference between the observed effects and the zero line is particularly relevant (assuming this line indicates that neither an attraction nor a repulsion are present), calculations of the effect size (ES) were performed. The ES holds identical significance as the test statistics however with emphasis on the meaningfulness of the effect rather than the sample size (Coe 2002; Field 2009; Sullivan and Feinn 2012). According to the criteria published by Sullivan and Feinn[26] (2012) the calculations of Cohen's d revealed a large ES for ISI 50 and 200 ms (d = 1.13) and ISI 16 ms (d = 0.87); a medium ES for ISI 100 ms (d = 0.68) and ISI 167 ms (d = 0.73); and a small ES for ISI 500 ms (d = 0.22).

ISI	Mean (SD) degrees	Mean (SD) arcmin	Sig
16	0.28 (0.66)	16.8 (39.6)	0.071
50	0.36 (0.65)	21.6 (39)	0.024
100	0.22 (0.64)	13.2 (38.4)	0.147
167	0.27(0.77)	16.2 (46.2)	0.126
200	0.31 (0.56)	18.6 (33.6)	0.024
500	0.05 (0.39)	3 (23.4)	0.598

Table 4-2 Mean and standard deviations of spatial bias for each ISI (in degrees of arc and in minutes of arc)

[26] Small EF (0.2); Medium EF (0.5); Large EF (0.8); Very large EF (1.3)

4.3. INTERIM DISCUSSION OF CHAPTER 4

The focus of the present chapter was to investigate cross-modal spatial perception, however in a different perspective from the classical way attention is studied: attentional effects are classically investigated by asking participants to attend (Klein 2004; either automatically or deliberately, Funes et al. 2005) to a region in space, where a task is performed. This means that the attentional deployment and behavioural performance are sharing the same spatial location. Facilitation effects have been observed, such as faster reaction times, increased accuracy and spatial resolution (Eriksen and Collins 1969a; Eriksen and Rohrbaugh 1970a; Colegate et al. 1973; Posner and Petersen 1989; He et al. 1997), but inhibitory effects have also been observed; such is the case of the inhibition of return effect (IOR; see Lupianez et al. 2006 for a review) which is characterised by a reversal of the attentional facilitation effect, in that after about 200 ms, responses are now slower and less accurate (possibly to prevent attention to go back to irrelevant locations, Posner and Cohen 1984; Tassinari et al. 1987).

The aim of the first experiment was to investigate the effects of visual attention on auditory spatial perception. More specifically, we asked if visual bias of auditory targets could be present in the case of visual auditory asynchrony, where attention is exogenously drawn to the visual modality. Participants were asked to judge the location of a sound and to ignore the preceding visual stimulus appearing randomly in the middle, left, or right. The results show a consistent visual attraction of the auditory target across ISIs: 1 - the size of the bias was shown to be independent of the direction of attention, which means that directing attention to the right hemifield attracted an auditory target in the same manner as directing attention to the opposite

hemifield. In other words, an attentional symmetry was present; 2 - the observed attraction was dependent on the temporal manipulations between cue and target. Specifically, the results show that the spatial attraction of an auditory target towards the side of a visual cue is biggest when the temporal delay between cue and target is 100 ms, gradually decreasing to fade away around 1.5 seconds of cue-target interval. Previous studies of exogenous spatial attention report that facilitatory effects of flashing a cue peak at 100-200 ms of cue-target asynchrony. This has been first shown by Eriksen and colleagues in the early 70s (Eriksen and Rohrbaugh 1970a; Eriksen and Hoffman 1972, 1973) using a leading cue paradigm and reaction times (RT) as dependant variables. RTs were shown to asymptote to an average maximum at around 100 to 200 ms of cue target asynchrony, suggesting a preferred window of operation for attentional facilitation. Attentional facilitation is classically shown either using measures of RT or some measure of performance, like accurately recognizing a target letter from a noisy environment (Colegate et al. 1973). In a spatial discrimination task, attention increases the accuracy of the spatial judgements, enhancing the localization of targets in the vicinity of the locus of attention (Driver and Spence 1998a, 1998b). However, as the present results show, rapidly attending to a location away from the locus of interest can lead to misrepresentations of space at the foveated location. Therefore, the cue-induced bias at the foveated location appears to be a side effect of exogenous orienting.

In experiment two, I aimed to extend the paradigm developed in the previous study and to investigate attentional spatial effects elicited by temporally close visual-auditory events. This was accomplished by applying interstimulus intervals (ISIs) that were able to sample with

more detail the interaction between a visual distractor and an auditory target. The new ISI range was: 16ms, 50ms, 100ms, 167ms, 200ms and 500ms. As in experiment one, the effect of bias was shown to be independent of the side where the visual distractor was displayed. The visual attraction produced by the left cue was identical to the attraction produced by the right cue, and for this reason, a single measure of bias (an average bias) was taken to quantify the spatial perception of auditory targets. A misrepresentation of space is evident, with the results showing auditory targets being attracted to the side where a previous visual cue was displayed (figure 4-9). A consistent visual bias of the auditory target has been shown for the majority of ISIs (from 16 to 200 ms), with ISI 500 ms showing the smallest effect size (see also table 4-2 for the mean and SD). This suggests that the spatial bias measured for ISIs 16 ms to 200ms is resolved around the 500 ms interval. More importantly, ISI 50ms and ISI 200 ms are the only intervals that show an effect size greater than 1, indicating that the visual attraction of auditory targets is a consistent and substantial effect at these delays. In the general discussion we will see how these two ISIs may be due to two different processes.

4.3.1. **Further experiments**

This chapter has shown that exogenous attention plays and important role in spatial perception. If this is true, then the same effects will be observed under other conditions of attentional deployment. To confirm the observed spatial bias of auditory space is due to attentional effects, a further study should adapt the paradigm to voluntary attention, and maybe other types of attentional modulation, such as sustained attention. However, care needs to be taken when designing the study to

avoid crossing the fine line between sustained attention and the effects of adaptation due to repetition (for example, Baldeweg 2006).

It has been assumed that the perception of stimuli simultaneity was maintained for ISIs 16ms and 50ms, based on previous studies, however, it would be important to disambiguate between synchronous and asynchronous stimuli, in future studies. A reliable way of doing so would be to use proven adaptive (or staircase) methods (Levitt 1970). These are often used to assess individual perceptual thresholds and, more specifically in our case, participants would answer in a two alternative forced choice manner if the two events appeared at the same time or at different intervals. This would have to be measured to each individual, jut before completing the experiment, since it is well know that environmental factors (even as ordinary eating and drinking; Dye et al. 2000; Fischer et al. 2002; Lieberman 2003) can influence a subject's cognitive performance. The same way it is essential to know when the cue and target events are perceived as temporally misaligned, it is also important to measure the perception of the targets without the presence of a distractor to serve as the baseline condition. Including a "catch trial" in the experiment (corresponding to a no-cue frame) would be a simple task and a measure of individual's unimodal unbiased perception would be available.

In summary, in the time course of our study we can probably witness several effects, each one happening at different temporal stages. To accurately represent the environment our brain has to integrate a multitude of stimuli in different modalities. It is, therefore, natural that for multisensory integration to be successful, the brain has to retain a certain flexibility or tolerance for events that occur temporally close, but for reasons of processing delay or mechanical transmission (such as in

vision vs audition) are not synchronous. This tolerance allows the brain, for example, to unify visual precepts with auditory ones, arising from a single multisensory event. Usually, vision leads this process as explain in the section 2.2 ("coding of space") and the auditory percept tends to follow visual inputs. A recent study sheds light into the results presented in this chapter. McGovern and colleagues studied the degree to which training influences this window of tolerance and showed that the classical ventriloquism effect can last up to 400 ms of SOA without training, but this window shrinks with training to 200 ms (lead or lag).

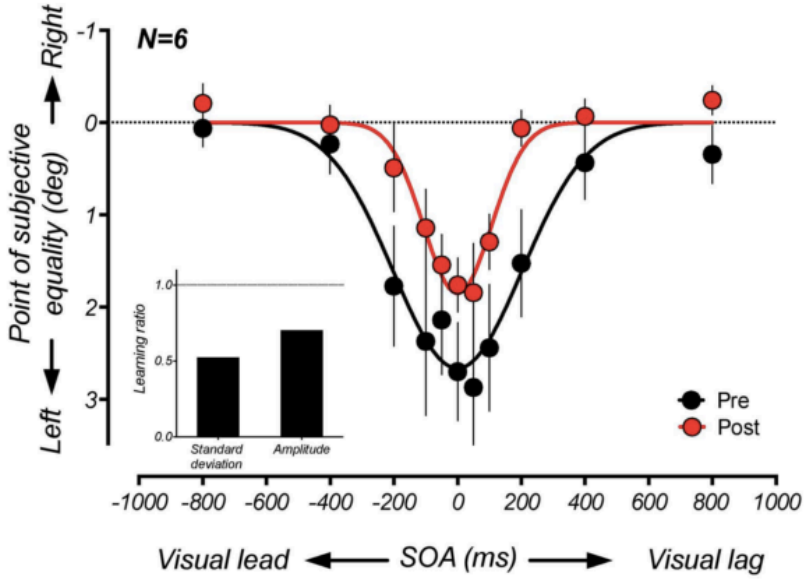

Figure 4-10 Ventriloquism effect as a function of SOA, before and after training, from (McGovern et al. 2016)

For this reason, the attentional attraction effect can only be responsible for the perceptual bias after 400 ms since before that, the ventriloquism effect is likely to dominate. At 1000 ms, the mislocalisation of auditory targets is likely explained by a spatial bias in the short-term memory trace. Lastly, the visual capture of auditory spatial cues was also shown to be resolved by 1500 ms.

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CHAPTER 5 AUDIO-VISUAL (AV) ARE

5.1. INTRODUCTION

In the previous chapter four we have seen that misrepresentations of space are also possible under crossmodal conditions. Shifts of a perceived location of a target away from its retinal position were reported in experiment 1 and 2. More specifically, the attraction of auditory objects towards the attention-grabbing visual cue was shown to peak at 100 ms of cue-target interval and decline thereafter, however it was still present at 500 ms. In the present chapter five I propose to study the reverse: the perceptual influence of irrelevant auditory cues on the spatial discrimination of visual objects (AV).

The attentional repulsion effect (ARE), developed by Suzuki and Cavanagh (1997), is a demonstration that lateralised visual flashes can effectively repulse centralised visual targets in a vernier display. Arnott and Goodale (2006) successfully replicated the classical ARE albeit for the left cue condition only as right cue shifts did not significantly differ from middle cues. Figure 5-1 illustrates one trial of the ARE paradigm adopted by Arnott and Goodale (2006). The original ARE effects was studied using 30 ms cues flashed in one of two diagonally opposite quadrants, as opposed to Arnott and Goodale's that only used one cue, and 60 ms, as opposed to 100 ms, targets. Furthermore, the cue-target interval (ISI) was set at 180 ms in the original study. Arnott and Goodale were successful in replicating the original ARE (left side path of figure 5-1). Moreover, replacing a visual cue with an auditory cue (broadband noise coming from left, upper middle or right positioned speaker) yielded similar repulsion results, although, auditory effects were smaller than those observed with the visual cueing.

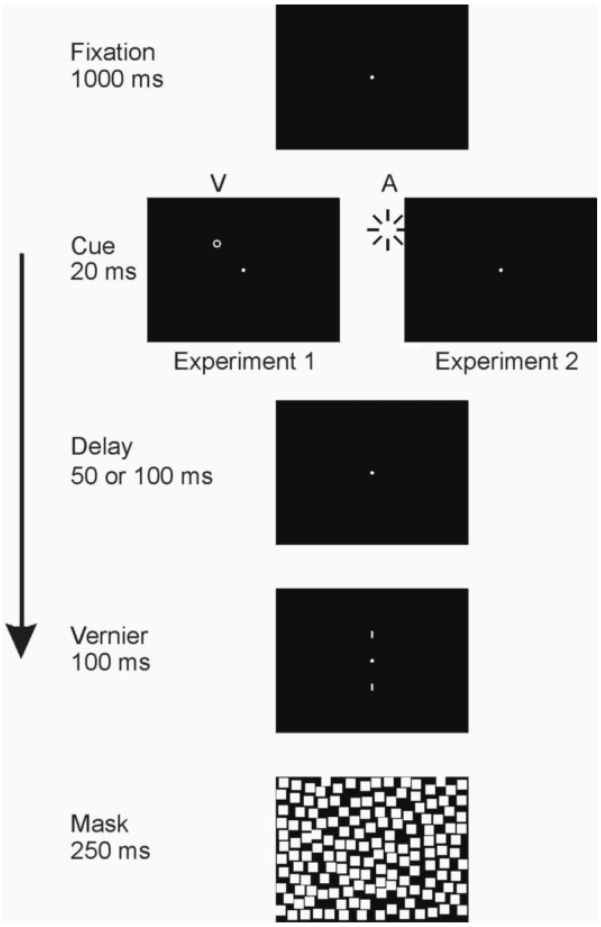

Figure 5-1 Sequence of one trial of Arnott and Goodale's (2006) attentional repulsion effect paradigm. Experiment 1 consisted in a visual circle presented in three positions (left, shown here; middle and right), above a vernier target display. In experiment 2, the visual cues were replaced by broadband noise. Reprinted with permission. License Agreement between the author of this thesis and Elsevier provided by Copyright Clearance Center ("CCC"). License number: 3840170606971.

Furthermore, the authors tested two ISIs (50 ms and 100 ms) and only found a significant repulsion at 100 ms. Nonetheless, the 50 ms ISI approached significance at $p = 0.07$, which seems to suggests that the effect takes more than 50 ms to depart from the neutral position. The authors did not investigate further temporal asynchronies, thus it is unknown whether the effect rises higher, remains in a plateau, or decreases, after 100 ms.

Since the ARE is thought to arise from cue-induced bias in retinotopic neurons in early visual areas (Pratt and Turk-Browne 2003; DiGiacomo and Pratt 2012), these results suggest that lateralised sounds can

influence the retinotopic response of the visual cortex despite eye movements not accounting for the attraction or repulsion (Arnott and Goodale 2006). However, despite the encouraging results from Arnott and Goodale's study, several methodological aspects need to be addressed. For instance, as argued in chapter three (General methods), it is important to only include data that meet certain criteria. This is particularly important in psychophysical experiments when the task is too difficult for a given subject and, as such, the predicted performance lay far from true observations. For example, looking at the left cue data, plotted in figure 5-2 from Arnott and Goodale (2006), the reader cannot be certain if the difficulty of the task was suitable for the population sample, as it appears that the fitted model (which was fitted to the average of all participants) does not reach 75% performance.

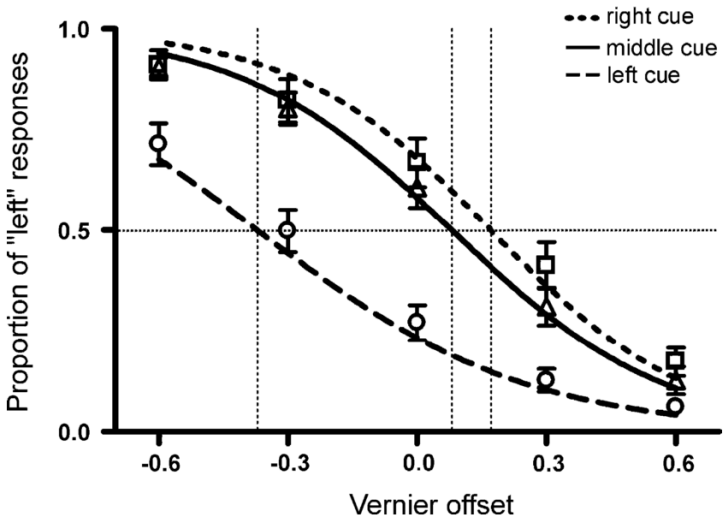

Figure 5-2 From Arnott and Goodale (2006) showing averaged responses fitted with a sigmoid function, across cue locations. Reprinted with permission. License Agreement between the author of this thesis and Elsevier provided by Copyright Clearance Center ("CCC"). License number: 3834291342703.

In the above example, one (or more) of the included participants could have a much bigger bias (even outside the possible physical range of the speakers), which in turn could alter the results. In fact the authors noticed that "the slope of the sigmoid for the left cueing condition was

different from that of the sigmoid for the right cueing condition ($p<0.05$)", when none of the remaining comparisons were different. The *third criterion* adopted in the present thesis was purposely design to avoid systematic measurement errors that could bias the study results. Another two exclusion criteria complement the above-mentioned one and can be review in *section 3.3.5*.

Another methodological aspect that is revised here is the location of the auditory cues. These cues were played through three speakers positioned around a computer screen. For this reason, the middle cue had to be elevated in relation to the other two cues because the speaker could only be positioned on top of the screen. The other two cues were played from the sides of the monitor. Thus, they were in the same vertical plane. Since human performance is worse in spatial discrimination in the vertical plane, when compared to the horizontal plane, (Middlebrooks 1992, 1997), the higher position of the middle cue (7.3° higher) could be introducing bias to the cueing effect. In addition, due to this elevation, the middle cue now possesses two salient features (the horizontal and vertical location), in comparison with the side cues that only possess one (their horizontal location), which could introduce a further unwanted spatial ambiguity to the middle cue. For example, by questioning why the middle cue is higher than the other two cues, the participants deployed more attention that allowed them to discriminate the vertical position of the middle cue in relation to the side cues. Since this is a behavioural experiment it is always unknown the participant's reasoning behind his/her answer, however, exogenous attentional mechanisms are intrinsically dependant on the saliency of the events, thus the need to control for this type of cueing influence.

Based on the above, the present thesis proposes a new paradigm to study the crossmodal ARE. In what follows I will describe the modifications to the Arnott and Goodale's paradigm. Firstly, the number of targets was increased to three on each side of the middle target (instead of 2) totalling 7 targets (instead of 5), which in practice will result in a regression estimation that is closer to true observations (since there are more sampling points of the behavioural response). Secondly, the middle cue was positioned in the same vertical plane as the other two cues to minimise the attentional and spatial ambiguity inherent to a salient event. Thirdly, six (6) interstimulus intervals (ISIs) were tested: from 16 ms to 500 ms. As it was suggested in the previous experiment (chapter 4), there might be two different mechanisms operating in such range of cue-target interval: one, at near synchrony (at 16 ms) to around 200 ms, related to exogenous cueing; and another at 500 ms which is the point where exogenous attention is no longer in operation. The aim here is to explore the time-course dependency of the cue-target interactions. According to the classical unimodal visual ARE (Suzuki and Cavanagh 1997) the repulsion effect rises until it reaches a maximum value at 200 ms, so I expect to see the same behavioural trend with crossmodal cues. Finally, the implementation of an inclusion/exclusion criteria comprised of three practical principles (described in *section 3.3.5* of the General methods chapter [3]) was also applied to ensure the study validity is preserved and systematic errors are reduced.

5.2. METHODS OF EXPERIMENT 3

This methods section holds many similarities with the methods previously described in the General Methods chapter and in the previous chapter four. The main difference between this experiment and the previous two behavioural experiments completed in the previous chapter is that now, the cue-target event is no longer visual-auditory, but the reverse: audio-visual[27]. Most of the detailed stimuli information, such as luminescence, radius of the visual cues, etc, can be found in the General Methods chapter (chapter three).

5.2.1. **Materials**

The materials used in this experiment were the same as the ones used in the previous chapter, comprised of a stimulating computer (that served as data acquisition unit as well), the infra red eye tracker (detailed description of its use can be found in the General Methods chapter, *section 3.2.1*), a chin rest, a computer screen, two speakers and a response box (see figure 3-1, in chapter 3, for a picture of the set up).

5.2.2. **Stimuli**

Stimuli consisted of an auditory cue and a visual target (AV). The details of the AV pairing used in this experiment as well as the respective calibration procedures can be found in the General Methods chapter three. Succinctly, the auditory cue was a short BBN (33 ms duration) that appeared randomly at one of three cue locations, each trial: middle, left, right. The visual target (66 ms duration) was the top vertical line of a vernier display, which assumed (randomly each trial) 6 linearly spaced positions around 0°. To avoid spatial information

[27] The bimodal pairing is classified throughout the thesis in the following order: AV refers to auditory cue and visual target, and VA refers to visual cue and auditory target

contained in the afterimages of the vernier targets (Suzuki and Cavanagh 1997; Arnott and Goodale 2006), masking squared were displayed from 250 ms. Both targets and cues appeared in the horizontal plane of 6.4°. This notion is illustrated in figure 5-3, below.

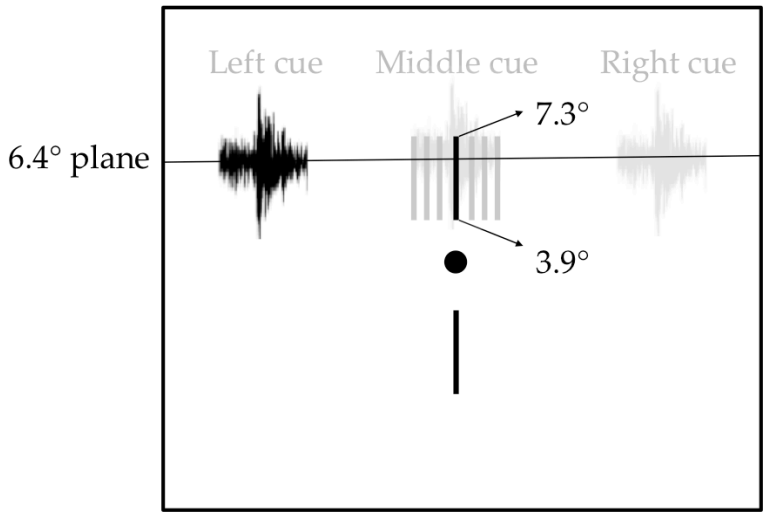

Figure 5-3 Relative positions of cue and targets as seen by the participant with reference to the 6.4° plane, where the centre of the speaker cones were positioned.

5.2.3. **Pilot Experiment**

In order to determine the range of targets a pilot experiment was conducted with five normal hearing and normal vision participants. Targets were seven linearly spaced lines between -0.6° (leftward targets) and 0.6° (rightward targets), equidistant from 0° (middle target). Both extreme positions of the targets were taken from Arnott and Goodale's study (2006), and the ISI was fixed at 167 ms. Figure 5-4 shows the average responses for all participants for each position of the target in each cue modality, on the right; and the fitted lines for all the cue positions of all participants, on the left. The key aim here was to check all data with the exclusion criteria, and to see if the task was too difficult or too easy by looking at the slope of the curve. The data from the five participants met all the inclusion criteria (or rather, they did not meet any of the exclusion criteria of *section 3.3.5* of the General Methods

chapter), thus, the same target positions were used in the main experiment.

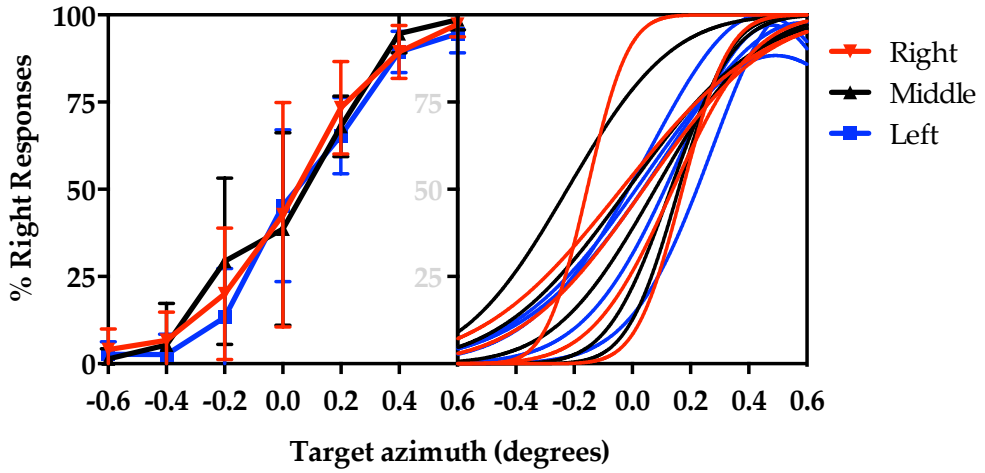

Figure 5-4 Left – Average responses of the five pilot participants for each target azimuth. Right – fitted models to the individual responses. Each colour represents a cue position; there are five curves per colour, one for each participant.

5.2.4. **Participants**

Thirty-one participants (12 males) with age ranging from 19 to 45 years (mean of 24.01, mode of 22), gave consent to take part in experiment 3. All participants completed a pure tone audiometry of 5 frequencies (described in *section 3.3.1* of the General Methods chapter) and had normal or corrected to normal vision. Data from one participant was excluded from further statistical analysis for meeting one or more exclusion criteria. The NLRMs fitted to this participant are depicted in figure 5-5, (details of the curve fitting methods are in *section 3.3.5*).

The reasons for excluding this participant are as follow: ISI 100 does not reach 75% performance of left targets for right cues (despite all curves showing acceptable GOFs) and ISI 500 does not reach 75% performance on all curves for right targets. Moreover, the fitted curve to left cues does not reach 0.7 of GOF, also at the longest ISI.

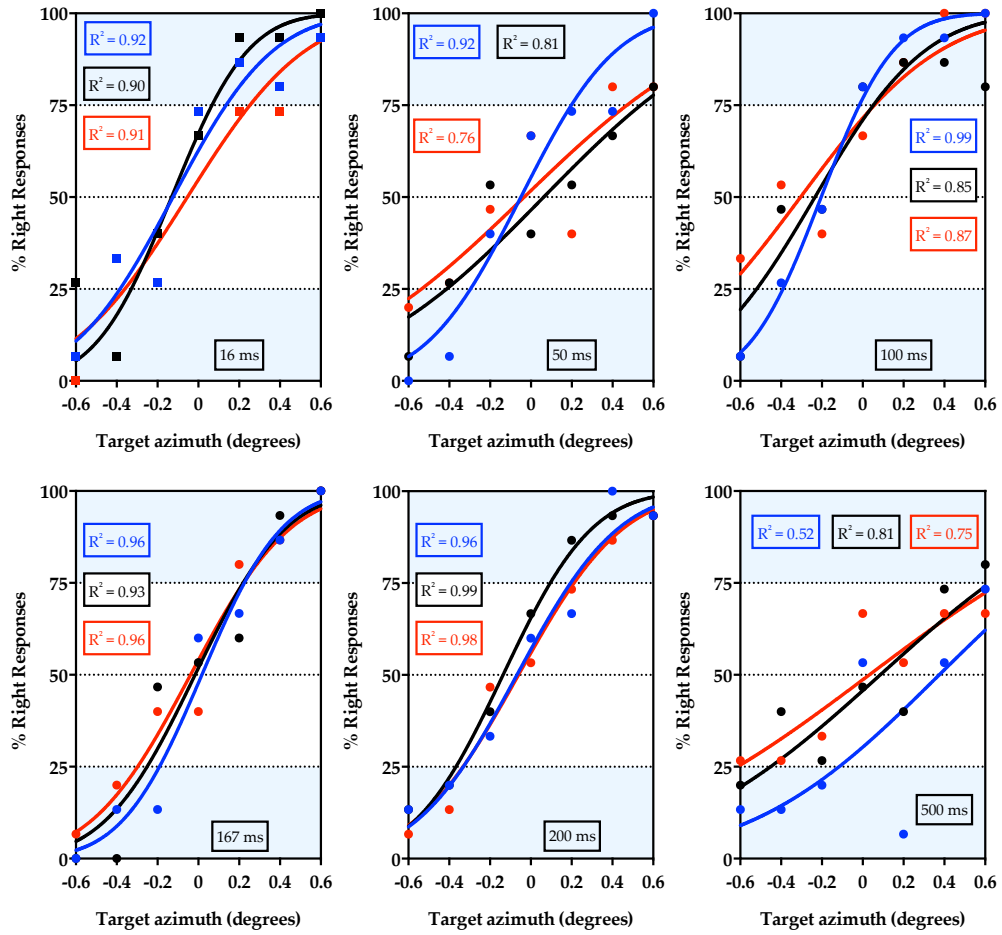

Figure 5-5 Excluded participant. ISIs 100 and 500 illustrate the reasons for the exclusion: failing to reach 75% performance in one or more fittings and/or a goodness of fit lower than $R^2 = 0.7$. • left; • middle; • right

5.2.5. Experimental Procedure

The experimental procedure was similar to the one described in experiment 1 of the previous chapter, *section 4.1.2*, but it will be summarised here for convenience. After completing a pure tone audiometry and completing the consent form, the participant was accompanied to a soundproof room and the experiment was explained using the card depicted in figure 5-6. The experiment consisted of a sound randomly presented each trial on the left, middle or right, followed by an ISI and two lines vertically aligned in a vernier display. To avoid afterimages from the vernier lines, a 250 ms mask of squares

was shown after the targets. The participant was required to ignore the first sound and to respond on a forced choice manner if to the top vernier line was to the left or right of the bottom line.

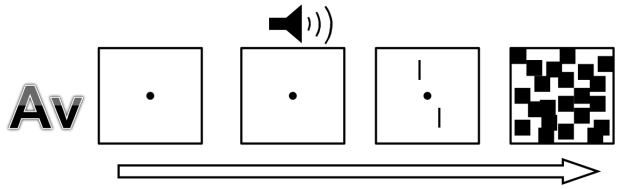

Figure 5-6 Card used to aid instructions to participants on the auditory–visual experiment 3.

The bottom vernier line was fixed at the centre and the top vernier line assumed 7 linearly spaced positions.

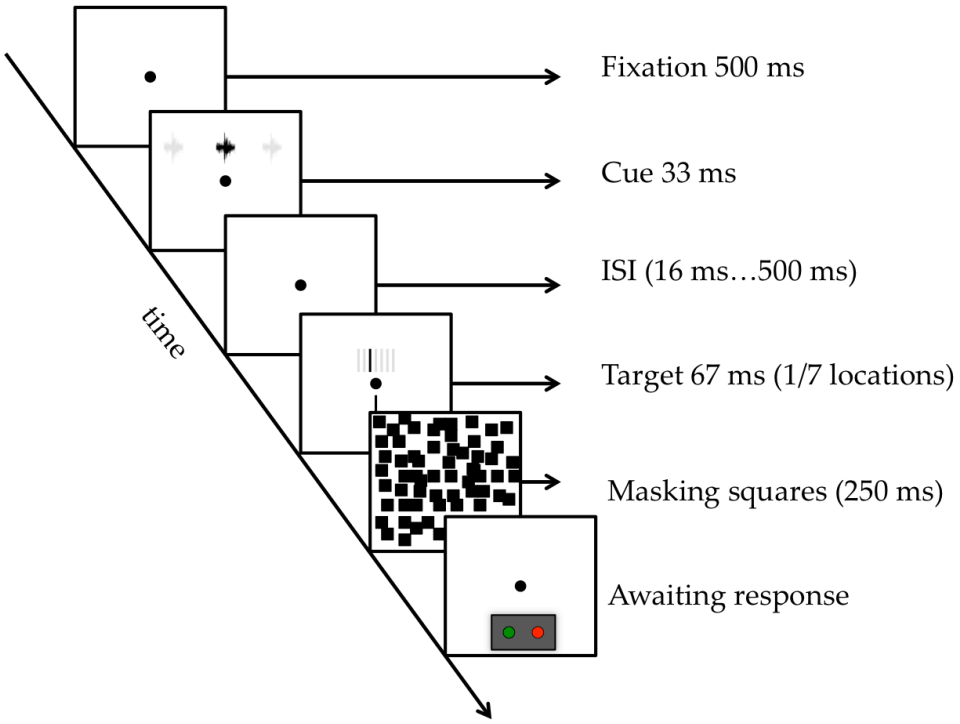

Figure 5-7 Sequence of events during one trial of experiment 3. Cue consisted of an auditory sound presented either in the left, right or middle and a visual target of two vertically displayed vernier lines. Participants completed 6 different inter-stimulus intervals (ISI), with each ISI comprising 315 trials (15 repeats per cue per target [15x3x7]).

Participants were told to keep their gaze on the fixation dot for the entire session. An infrared eye tracker was used to ensure fixation was correct, and a chin rest was used. After a practice run of two trials per

target under dark room conditions, participants were left alone in the booth. The experiment began after calibration of the eye tracker. The participants completed six sessions, one per ISI, which were randomly assigned. The sequence of events of one trial is depicted in figure 5-7.

5.3. RESULTS OF EXPERIMENT 3

The data analysis for this experiment follows the same pipeline as in the previous experiment. Figure 5-8 illustrates this pipeline with three main steps: the averaging of the responses, the NLRM fitting with extraction of the points of subjective equality (PSEs) and the statistical analysis. Each cue position and each target position are averaged across the 15 trials for each individual. The PSE were calculated according to the general data analysis procedures detailed in *section 3.3.4* of the General Methods chapter. PSEs were then imported into SPSS (IBM® SPSS® Statistics 22.0.0.0) for statistical analysis.

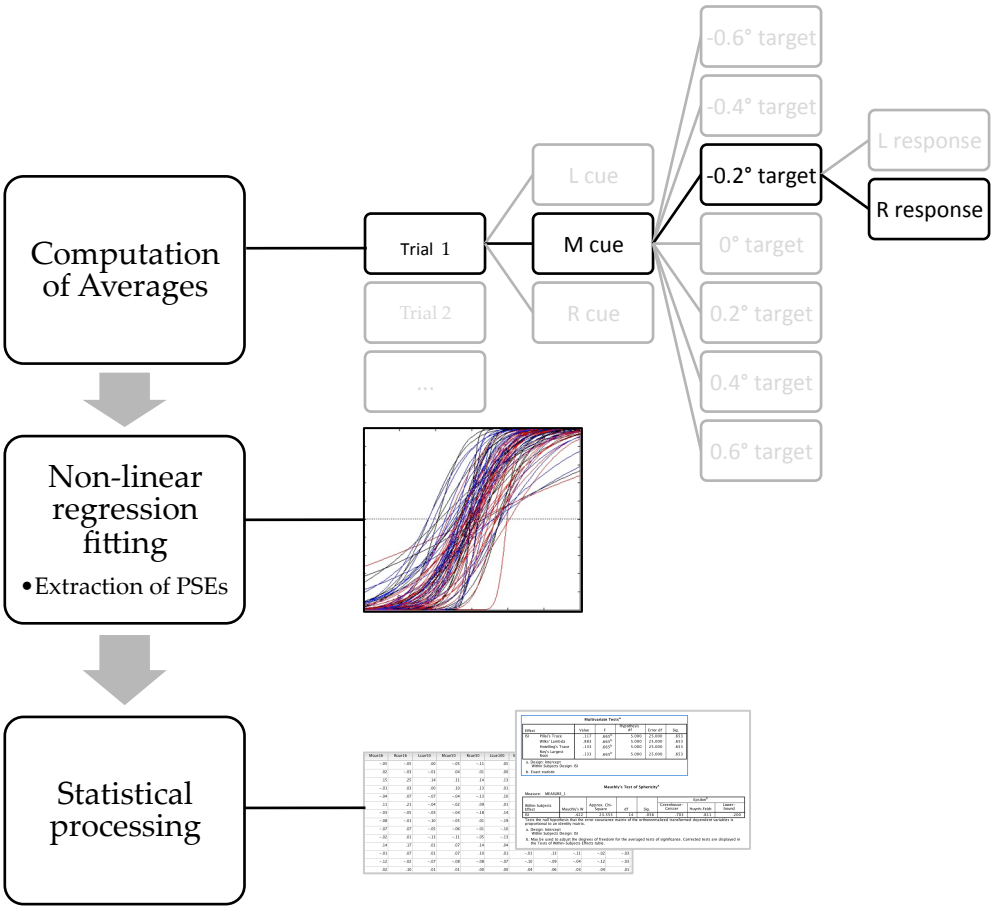

Figure 5-8 Pipeline of the data analysis. Each recorded response (one per trial) is added and averaged, for each target at each cue location. Averages are then converted to a percentage of left responses. A non-linear regression model is then fitted to the averages of each target. Three models are fitted, one for each cue location (L, M or R), per participant, for each ISI. The PSE is then extracted from the model and imported to SPSS for statistical processing.

A measure of bias was created, that corresponded to: left bias = left PSE – centre PSE; right bias = centre PSE – right PSE. A repeated measure analysis of variance (ANOVA) with ISI (6 levels: 16, 50, 100, 167, 200 and 500 ms) and bias side (2 levels: left bias and right bias) as the within-subject factors revealed a significant main effect of bias side $F(1, 29) = 5.17$, $p = 0.03$. There was no main effect of ISI $F(5, 145) = 0.456$, $p = 0.808$, and the interaction between ISI and bias side was non-significant, $F(5, 145) = 1.643$, $p = 0.152$ (Greenhouse-Geisser corrected). In other words, ISI had no main effect on the spatial perception of naïve participants, however the exogenous cueing (left or right) was further investigated with post-hoc tests. A paired-samples t--test was used to investigate cue side differences at each ISI (figure 5-9). A significant difference was found at ISI 500 ms $t(29) = 2.1$, $p = 0.04$. This indicates that at 500 ms of cue-target interval, flashing a cue at the right yield significantly bigger[28] bias (M = -0.0538; SE = 0.1) than the left cue (M = -0.0068; SE = 0.1).

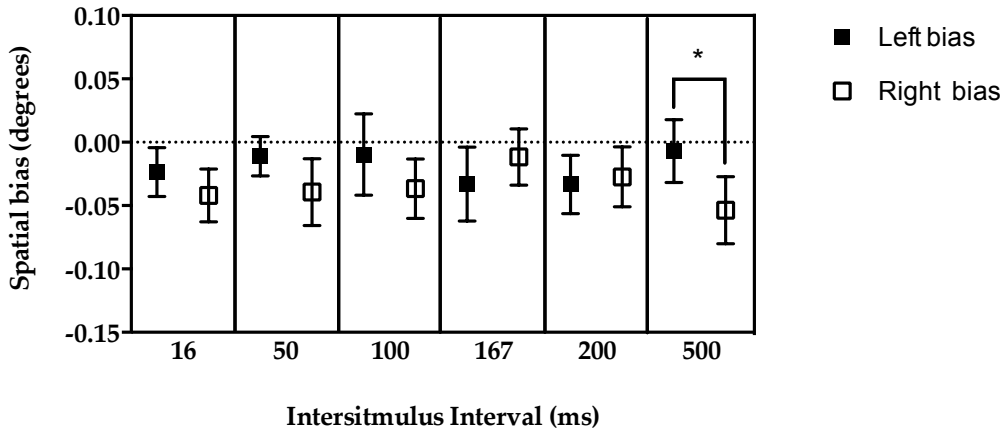

Figure 5-9 Comparison of left and right bias across ISI. A paired samples t-test indicated a significant difference between the two cue sides at 500 ms. Results are in angular degrees. Error bars represent SE.

[28] Bias refers to the departure from 0°. The bias induced by the left cue is closest to 0°, thus has the smallest bias.

Care must be taken when interpreting this significant difference because the effect size was calculated at r = 0.36 (a small effect size). The remaining pairs were not significantly different from each other, which indicates that the bias induced by the right or to the left cue did not differ in magnitude. A one-sample t-test was used to verify if the bias induced by the left and right cue differ from 0°. The left bias was not found to be significantly different from zero t(29) = -0.57, $p = 0.58$, but, inversely, the right bias was t(29) = -4.22, $p<0.001$. Due to the non--significant difference of the left and right cue for the remaining ISI, and for the sake of increasing statistical power, both left and right bias were averaged for ISIs 16, 50, 100, 167 and 200 ms. This can be reviewed in figure 4-7 (also in the appendices) and can also be found in the text that immediately precedes it. A section (8.2.2) in the general discussion of this thesis will address this issue. In line with the analysis of the previous chapter, results were transformed to minutes of arc to allow comparisons with the literature.

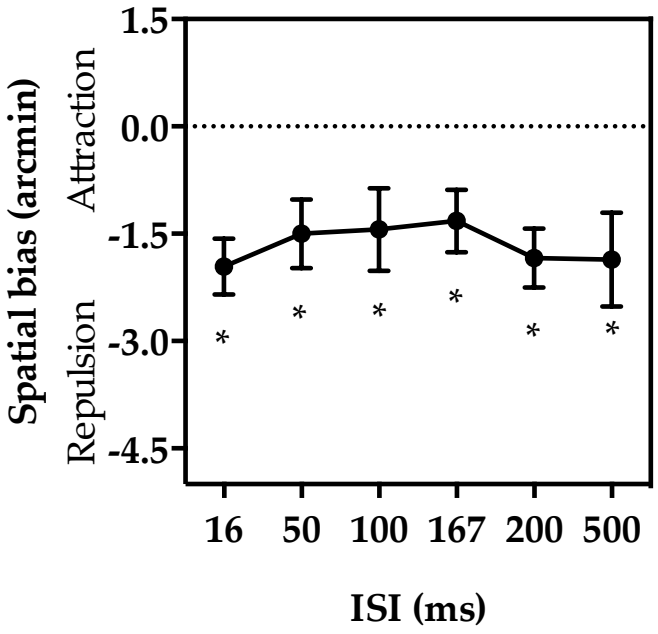

Figure 5-10 Average spatial bias across ISI. The bias induced by a visual cue on an auditory target does not change with the temporal interval between them. Asterisks represent a statistically significant difference from 0°. Both bias for 500 ms ISI were averaged for

illustration purposes. Un-averaged data can be found in the previous figure (4-7). Error bars are SE.

An ANOVA with ISI as the single factor (6 levels: 16, 50, 100, 167, 200 and 500 ms) was used to investigate the main effect of ISI. The Mauchly's test of sphericity specified that sphericity was assumed, thus no corrections were applied. The results from the ANOVA show there was no main effect of delay $F(5, 145) = 0.456$, $p = 0.808$, which indicated that the averaged bias does not change with ISI. This can be seen in figure 5-10 which illustrates the consistent spatial repulsion across ISI.

A one-sample t-test was used to confirm the repulsion. Results were adjusted using the Holm-Bonferroni method (a less stringent method to the classical Bonferroni). A detailed description of this method can be found in the results section of experiment 1. Table 5-1 illustrates the resulted significance value and the adjusted value, with asterisks denoting significant comparisons.

ISI (ms)	Average bias (SE)	*p* value	Adjusted alpha
16	-1.98 (0.4)	0.000	0.008 *
50	-1.5 (0.5)	0.003	0.017 *
100	-1.44 (0.6)	0.019	0.050 *
167	-1.32 (0.4)	0.005	0.025 *
200	-1.84 (0.4)	0.000	0.010 *
500	-1.86 (0.3)	0.000	0.013 *

Table 5-1 The ISI and respective *p* values were compared to an adjusted alpha using the Holm-Bonferroni correction. Asterisks mark the significantly different comparisons.

5.4. INTERIM DISCUSSION OF EXPERIMENT 3

The general aim of the present experiment was to test the influences of exogenous attention on crossmodal spatial perception. A unimodal visual ARE paradigm was adapted by Arnott and Goodale in 2006 to investigate if the effect would be maintained under crossmodal conditions. The present experiment modified Arnott and Goodale's paradigm with the purpose of extending and improving it on several methodological aspects. The specific aim of this experiment was to study the crossmodal audio-visual ARE under several conditions of cue and target interval, from 16 ms to 500 ms. This novel aspect of the study would allow investigations under the entire widow of exogenous attention until after it has declined (at 500 ms). Another specific aim was to address some of the methodological concerns found in the above-mentioned study (raised in the introduction). Furthermore I aimed to complement the results of Arnott and Goodale's study by using a different method of data analysis, which could also confirm previous reports that the ARE is reliable and of easy reproducibility (Pratt and Arnott 2008).

This discussion has been divided in two sections. The first section will discuss the results found in the present experiment, relating the findings to the literature whenever possible. The second section will address the methodological differences between Arnott and Goodale's (2006) study and this thesis.

5.4.1. **Discussing the results of experiment 3**

The results consistently show a repulsion of auditory targets away from the location of a previous displayed visual cue. This repulsion was present in all ISIs and did not present a distinct peak in bias magnitude.

The crossmodal ARE was also shown to be independent of manipulations of ISI. One unexpected result was the significant difference in left and right bias at 500 ms. This difference was addressed by averaging the left and right biases, however, a specific section in the general discussion is devoted to discuss possible explanation for that significant difference.

At 100 ms, the authors report much larger repulsion values than the ones reported in this study. For example, Arnott and Goodale's left cue mean was 7.8 arcmin and the right cue was 4.2 arcmin[29]; while in the present experiment, the left bias observed was 1.8 (SE 1.2 arcmin) and the observed right bias was 1.2 (SE 1.14 arcmin). There are several reasons that might have contributed for this discrepancy. First, the auditory cue used by Arnott and Goodale was a broadband noise burst with a frequency range of 20-20000 Hz, whereas the one used in this study was a narrowband burst filtered between 200 Hz to 1200 Hz. Normal hearing participants can point to brief broadband noise burst with considerable accuracy, but, when comparing that performance with localising narrowband sounds, there are systematic localisation errors (Makous and Middlebrooks 1990; Middlebrooks 1992). It could be that our auditory cues were less efficient in pulling the participants' attention. Second, Arnott and Goodale presented the auditory cue at a lateral distance of 18° from the centre, while our auditory cues were positioned at 10° from the centre of the screen. The greater separation of the cues could have produced a bigger spatial repulsion, which seems to suggest that increasing the distance between cue and targets could increase the size of the ARE. On the one hand, if the above is true, it would indicate that the crossmodal ARE can be modulated by changing

[29] The authors did not report any measure of dispersion

the spectral and spatial components of the cue. On the other hand, it would be important to investigate at what eccentricities the crossmodal ARE operates because the classical unimodal visual ARE (Suzuki and Cavanagh 1997) is fairly robust to manipulations of the distance between cue and target. But, Kosovicheva et al (2010) tested the effect's dependency to cue-target distance (up until 12° of separation) and found that the effect increases in magnitude up to four degrees of separation, decreasing linearly after that. If we take this evidence into account, 10° of separation (in the present experiment) would have yielded a bigger bias than 18° (from Arnott and Goodale's study). Clearly this is a debatable area that needs further research to better characterise the ARE phenomenon. Third, it is unknown what inclusion criterion was used by Arnott and Goodale in the psychometric fitting of regression models. The authors only divulge that the GOF (goodness-of-fit) was very good (with R^2 indices above 0.94), but, as discussed in the general methods chapter (2), a straight line can have good R^2 values and be a bad predictor of behavioural psychometric performance. Revisiting figure 5-2 in the introduction of this chapter, the authors fitted a sigmoid curve to the grand average of all participants, but the left cue appears to not reach (or barely reach) 75% performance, therefore some of the participants that were included in this fitting would have been rejected in this thesis (see exclusion criteria 3, general methods chapter 3, *section 3.3.4*). It is possible that including these participants could have inflated the average repulsion.

Lastly, the present results suggest that the crossmodal ARE does not change with variations in the temporal interval between cue and target. To my knowledge this is the first study that demonstrates this independent relationship between cue-target interval and bias

magnitude and polarity in the crossmodal ARE. Arnott and Goodale (2006) have tested 2 ISIs (50 ms and 100 ms) but did not investigated the entire range of operation of exogenous attention. Furthermore, they report non-significant results at 50 ms, consequently, it is difficult from their study, to deduce if the same trend is present.

5.4.2. **Discussing the new methodology**

This section is aimed at discussion the methodological changes implemented in the new crossmodal ARE paradigm. The present experiment (3) shares two ISIs with Arnott and Goodale's 2006 study: the 50 ms and the 100 ms, however, Arnott and Goodale did not find any statistically significant bias at 50 ms. Because the authors did not report effect sizes, it is hard to interpret their findings, though they explained that "there was a trend for the V50[30] for the left cue to be significantly lower than the theoretical 0 ($t(1,19)=-1.6$, $p<0.07$); however, neither the V50 for middle cue nor the V50 for the right cue were different from 0 (both $p>0.1$)", (p.1556). At 100 ms, the authors reported a significant difference between left and right cueing. This is the first confirmation that the unimodal visual ARE is also possible across modalities; more specifically under auditory cueing and visual targeting. Notwithstanding, this tells us little more about the size of the bias in each hemifield. It is merely an index of departure from zero. If the left cue is -7, the middle cue -5 and the right cue -3, this does not mean that the bias induced by the left cue is -7, as clearly the subjective performance of the participant is shifted to the left, regardless of cue position. Also, the fact that the left cue presented an average bias that is more negative than the middle and right cue is to be expected due to the nature of the task. Let us revisit figure 3-11 from the general

[30] V50 = PSE; results are from a one-sample t-test comparing PSEs with 0

methods chapter (pasted below for convenience). In case of a spatial repulsion, a left cue will always induce a more negative bias when compared to the middle or right cue.

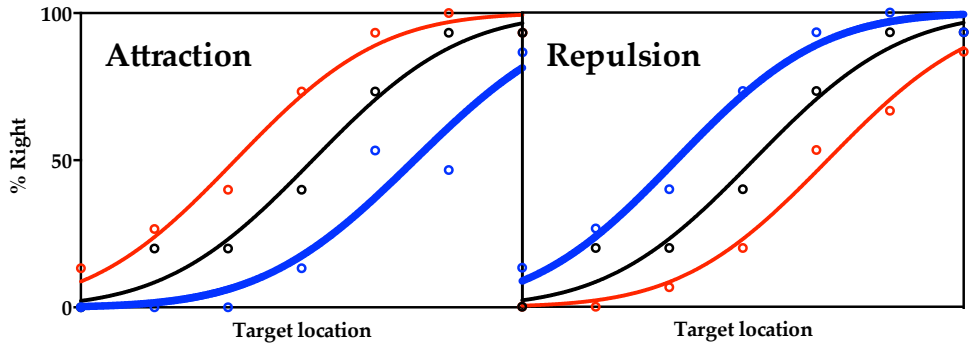

Figure 3-11 Examples of plots of attraction and repulsion of an auditory target that was preceded by a visual cue. Blue is left cueing, black is middle cueing and red is right cueing.

If there is a difference in cueing effects it only means that one of the cues was successful in inducing a spatial bias; whereas, if all cues induce an equally negative bias (meaning the PSEs for the three cue positions are all negative and not significantly different), it would indicate that the spatial perception of the participant is always offset (at least from the perspective that the middle is at 0°) since there is no difference to the middle cue. But, there is an important concept masked behind the assumption that a middle cue produces neither a repulsion nor an attraction. In fact, the middle cue seems to resolve the natural overestimation of the left side that is present in neurologically normal and healthy individuals: the pseudoneglect phenomenon. Toba et al (2011) have shown that (in a line bisection task) when no cue was presented before the line, the PSE of an horizontal line bisected by a vertical line was 3.22 arcmin to the left. This means that the participants perceived the transector to be more rightward than its true position. In the same study, Toba and colleagues have shown for the first time that the unimodal visual ARE is possible with line bisection tasks. The

pseudoneglect phenomenon (Bowers and Heilman 1980) is characterised by attention being more strongly directed to the left side. This is because the right hemisphere preferentially controls visuospatial attention (see introduction of Siman-Tov et al. 2007). As a result of overattending to the left hemifield, a spatial bias consistent with the ARE can be behaviourally revealed. The pseudoneglect phenomenon is classically studied using line bisection tasks, thus to truly measure the spatial perception of the vernier targets without cueing, further experiments would have to include a catch trial, where no cue would be presented (but I would predict a leftward bias, consistent with the pseudoneglect phenomenon). If the pseudoneglect effect is also present with a vernier target then the results from the present experiment[31] and from Arnott and Goodale's (2006) study would suggest that the natural left bias can be resolved by using a middle cue. Furthermore it would have methodological implications in future studies using the crossmodal ARE as, for example, the t-tests performed by Arnott and Goodale's (2006) comparing the bias with a virtual value of 0° would have to be substituted by *X*° (with *X* being the result from the no cue condition), as that would be the true central perception of each participant.

The methodological changes to Arnott and Goodale's (2006) paradigm adopted in this chapter also encompass statistical decisions. Arnott and Goodale used the raw PSEs extracted from the psychometric fitting to perform statistical inferences. Therefore, the authors had three levels of the independent variable cue positon: a left cue, a middle cue and a right cue. However, the authors did not compute a measure of bias and

[31] A further one sample t-test was used to compare the PSE of the middle cue against 0, across ISI. The results are in the appendix of this chapter and show no differences between the middle cue and zero.

assumed that the perception of middle was the same when presenting a middle cue. In contrast, in the analysis section of the present chapter the middle cue was used as a way to normalise the bias results (by subtracting the left and right PSE to the middle PSE), without assuming that the middle cue would result in a neutral spatial perception (0°).

Both studies (Arnott and Goodale 2006 and the present chapter) present a middle cue and are the first studies that do so in a crossmodal ARE paradigm. Arnott and Goodale used three physical speakers to present the sound, and as such, the middle cue had to be elevated in relation to the other cues (middle speaker was positioned on top of the screen). For this reason, the middle cue possessed two salient features, the vertical (coming from the top of the computer monitor) and the horizontal position (middle), whereas the side cues only differed in their horizontal positions (left or right; the vertical position was aligned in the same plane). It is possible that the middle cue created some spatial ambiguity and confusion to the participant, as the middle cue was presented 7° higher than the side cues (15.8° for middle cue and 8.5° for side cues). To address this issue, the new paradigm developed in this thesis used stereo level differences to create the location of audio targets, and as such, the middle cue was presented in the same vertical plane as all the other stimuli. Furthermore, the participant was informed that there was one of three events preceding a target: a left a middle and a right one. Even though I explained that these events had no relation to their task and should be ignore, it was important to disambiguate between the three locations to prepare the participant to the events that followed. Debriefing the participants revealed that indeed they perceived a central, a leftward and a rightward cue and that they ignored it. Moreover, all participants indicated that sometimes

cues were not fully perceived[32], supporting the notion that attentional shifts are not always accompanied by awareness (Mulckhuyse et al. 2007). This is most likely related to the endogenous attentional deployments demanded by the discrimination vernier task.

In summary, I have successfully extended Arnott and Goodale's (2006) study of the crossmodal ARE. I have shown that the effect can be elicited under several conditions of cue-target asynchrony, which demonstrates its reliability. The present experiment supports the notion that the crossmodal ARE is a robust effect, and as such, it might be worth considering it as a tool to quantify the capture of crossmodal attention, in the same way as Pratt and Arnott (2008) suggested for the unimodal visual ARE.

[32] In certain trials participants could not remember if there had been an auditory cue or not.

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CHAPTER 6 THE UNIMODAL ARE

6.1. EXPERIMENT 4 – THE VISUAL ARE

6.1.1. Introduction

The aim of this experiment is to reproduce the visual ARE to establish context with previous repulsion studies. Furthermore, in doing so, I aim to clarify the time-course of the ARE. There are scattered results that point to a general time frame where the effect lives; for example, Arnott and Goodale (2006) investigated 50 and 100 ms ISI, but because there was no effect found at 50 ms, the data from both ISIs was merged in a single analysis. As we have seen in chapter 3, several mechanisms could be present at several ISIs, thus merging two ISIs might mask or decrease the presence of a possible effect at other ISIs. Others have used a single 50 ms ISI (DiGiacomo and Pratt 2012; Gozli and Pratt 2012), a single 150 ms ISI (Kosovicheva et al. 2010) and a single 200 ms ISI (Chow et al. 2014). Two studies used 13 ISIs to track the effect, however, one study used a sample of two participants (including the author of the study, Suzuki and Cavanagh 1997) and the other study used an unconventional method to correct for multiple comparisons (the Ryan's method Ono and Watanabe 2011). Therefore, it is open to debate how the ARE behaves across time, since few studies have investigated the time-course of the ARE in a single experiment with one paradigm. In this experiment we aim to investigate the behaviour of the ARE by parametrically varying the time interval between cue and target. Six ISIs were used: 16 ms, 50 ms, 100 ms, 167 ms, 200 ms and 500 ms. We predict that, since attentional effects have a very distinct time-course (with facilitation giving rise to inhibition at the 200 ms CTOA mark), a part of this behaviour should transpire to the ARE, further supporting

the notion that attentional mechanisms are behind these spatial mislocalisations. Considering attention moves away from the cue after 150-200 ms and if the ARE is due to cost of shifting attention away from the retinal position, then we should observe a presence of an ARE that rises from 16 ms to 167 ms, peaking at around 167 and 200 ms and declining thereafter.

Finally, studies like Suzuki and Cavanagh (1997), Ono and Watanabe (2011), Chien et al. (2011), and others, have used opposite diagonal cues, thus making it harder to accurately quantify the size of cue-induced bias, considering that there is no measure of the central bias inherent to each individual. If the ARE is to be used in the future as a measure of attention deployment, as suggested by Pratt and Arnott (2008), a quantitative measure needs to be calculated from the ARE. Therefore, the present experiment will additionally measure the central bias by means of a three-cue (left, centre and right) paradigm, introduced in the previous chapters. To try to build a consensus between the different paradigms used to elicit the ARE, we will use the same paradigm developed in chapter three (that successfully evoked the crossmodal ARE) to elicit the original unimodal visual ARE reported Suzuki and Cavanagh (1997), and to further adapt it in experiment 5 to investigate the ARE in unimodal auditory conditions.

6.1.2. **Methods of experiment 4: the visual ARE**

The methods described in this section contain many similarities with the previous experiment, and the majority of stimuli and paradigm implementations have already been described in previous chapters. Nevertheless, for convenience, I shall summarise relevant information in order to facilitate the understanding of the experiment here described.

6.1.2.1. Participants

A total of 24 participants (age range 19-58 years, mean of 26.17 years, mode of 22) took part in this study. Participants were naive to the purpose of the study and had normal hearing, confirmed by a five frequency pure tone audiometry: 250 Hz, 500 Hz, 1 kHz, 2 kHz and 4 kHz and normal, or corrected to normal, vision. Seven participants were excluded from the study for not meeting the inclusion criterion mentioned in section 2.3.4 of the general methods chapter, and a further participant did not complete a full data set, thus not included in the total participant count. Participants were tested individually and provided informed consent prior to inclusion in the experiment.

6.1.2.2. Materials

The materials used in this experiment were the same as the ones used in the previous chapters. This comprised a stimulating computer (that served as data acquisition unit as well), the infrared eye tracker (detailed description of its use can be found in the General Methods chapter, *section 3.2.1*), a chin rest, a computer screen, and a response box (figure 3-1, below, is a picture of the experimental set up).

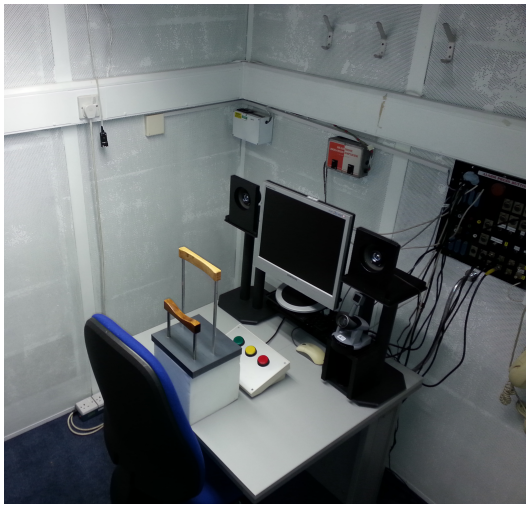

Figure 3-1 Prototype of experimental set up in a soundproofed room. Chin rest and response box was fabricated in-house. Speakers were later enclosed in a custom built closed baffle to minimise the effects of wave cancellations.

6.1.2.3. Stimuli

The main difference between this chapter and the previous three behavioural experiments of the previous chapters is that now, the present experiment investigates unimodal spatial interactions: visual-visual and auditory-auditory. The present chapter is concerned with replicating and extending Suzuki and Cavanagh's ARE paradigm. Thus, the cue-target event is no longer crossmodal, but unimodal visual (VV[33]). The details of the VV pairing used in this experiment as well as the respective calibration procedures can be found in the General Methods chapter (three; section *3.3.3*), but succinctly, the visual cue (33 ms duration) was a circle randomly displayed at three locations, each trial: left, right and centre. The visual target (66 ms duration) was the top vertical line of a vernier display, which assumed (randomly each trial) 6 linearly spaced positions around 0°. To avoid spatial information contained in the afterimages of the vernier targets (Suzuki and Cavanagh 1997; Arnott and Goodale 2006), masking squared were

[33] Visual cue; visual target

displayed from 250 ms. Six interstimulus intervals (ISI) were tested: 16 ms, 50 ms, 100 ms, 167ms, 200 ms and 500 ms.

Both targets and cues appeared in the horizontal plane of 6.4°. This notion is illustrated in figure 6-1, below.

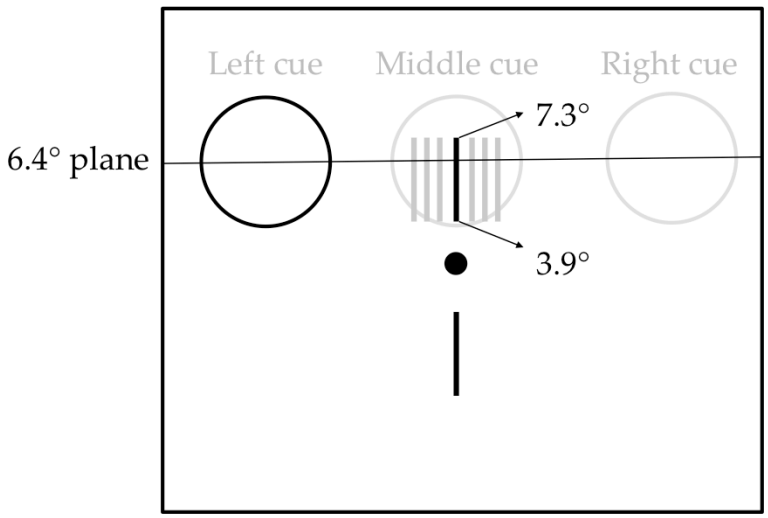

Figure 6-1 Relative positions of cue and targets as seen by the participant with reference to the 6.4° plane, where the centre of the speaker cones were positioned.

The targets used in this experiment had previously been subjected to piloting in the previous chapter five. The reader is referred to *section* 5.3.2 that contains data from the pilot experiment that led to this choice of targets. Further information such as luminescence, radius of the visual cues, etc, can be found in the General Methods chapter.

6.1.2.4. Experimental Procedure

The experimental procedure adopted in this experiment was similar to the one described in chapter four (*section 4.1.2*). In summary, the participants completed a PTA exam to confirm normal hearing function, and sat in a chair in front of a computer screen, in a sound treated room. The experiment was explained with the help of a card, depicted in figure 6-2. A visual cue (circle) was flashed at one of three locations, randomly each trial.

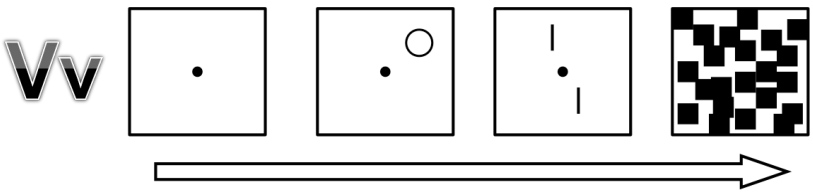

Figure 6-2 Card used to aid instructions to participants on the visual ARE experiment.

A target consisted of a top line in a vernier display followed the cue (circle). The participant was asked to judge is the top line was to the left of right of the bottom line by pressing the corresponding button in the response box. The participant was asked to ignore the flashed circle, as it did not contribute to the events that followed it. The bottom vernier line was fixed at the centre of the screen and the top vernier line assumed 7 linearly spaced positions. After the presentation of the vernier target, a masking image containing 250 randomly assigned squares was displayed for 250 ms.

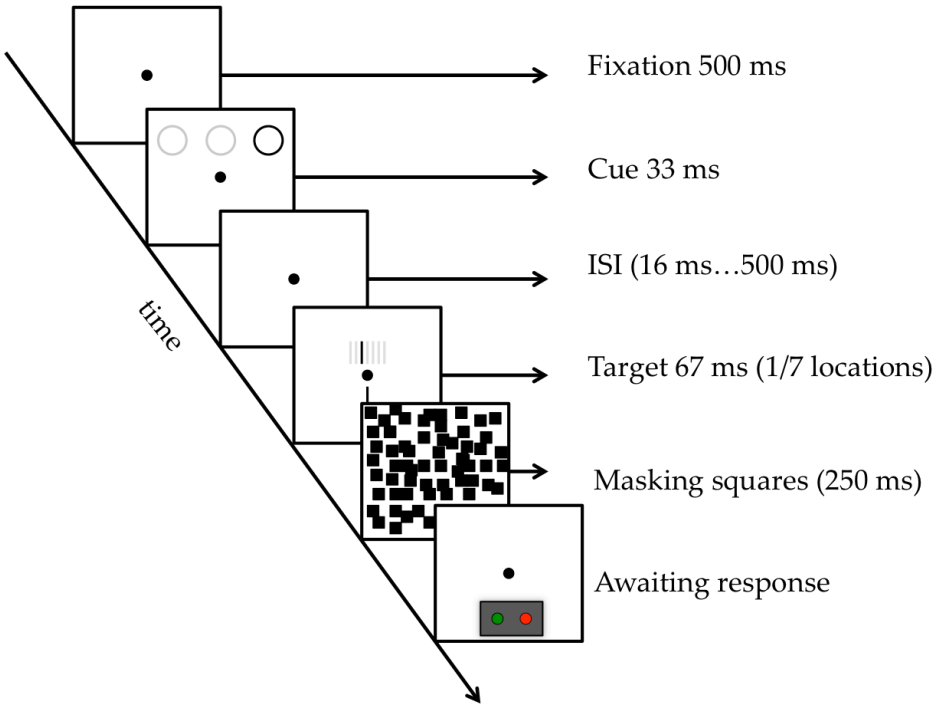

Figure 6-3 Sequence of events during one trial of the visual ARE experiment. Cue consisted of a circle presented either in the left, right or middle and a visual target of two vertically displayed vernier lines. Participants completed 6 different inter-stimulus intervals (ISI), with each ISI comprising 315 trials (15 repeats per cue per target [15x3x7]).

An infrared eye tracker was used to ensure fixation was maintained in the centre of the screen. Each participant completed six sessions, one per ISI, which were randomly assigned. Figure 6-3 illustrates the events contained in one trial. Due to the difficulty of the task, participants were allowed a maximum of one practice run comprising of two trials per target azimuth, in each condition, or until the tester was confident the participant understood the instructions. The participants were left alone in the dark and after calibration of the eye tracker the participants completed the experiment consisting of 315 trials per ISI (15 repeats per cue [3] per target [7]). Participants completed six sessions, one for each ISI (16 ms, 50 ms, 100 ms, 167 ms, 200 ms and 500 ms). The order of the sessions was randomised for each participant.

6.1.3. **Results of experiment 4 – visual ARE**

The data analysis of the current experiment follows the same model adopted in the previous chapters. In appendix C.6.2, the reader can find a figure of the general pipeline, for convenience, but in summary, after collecting the responses from the participants, the data was transformed in proportion of right responses (expressed as percentage). This process was done individually for each participant, for each target (n=7), in each cue position (n=3), in each ISI (n=6). This yielded a large data set grouped according to ISI. A NLRM was fitted in order to extract the PSE that corresponded to a given participant in a given cue position of a given ISI. PSE values were then exported into SPSS (version 22.0.0.0; IBM® SPSS® Statistics) and converted to minutes of arc to allow comparisons with Suzuki and Cavanagh (1997). Data was further transformed by computing a new variable: a left or right bias that corresponded to the left PSE minus the middle PSE, in case of the left bias; and the middle PSE minus the right PSE, for the right bias. This measure of bias had not been computed by Suzuki and Cavanagh (1997).

A repeated measure ANOVA with bias side (2 levels: left bias and right bias) and ISI (6 levels: 16, 50, 100, 167, 200 and 500 ms) as the within-subject factors revealed that there was no main effect of bias side $F(1, 23) = 0.191$, $p = 0.66$. In other words, no differences were found between the bias induced by the left cue and the bias induced by the right cue. In an attempt to increase statistical power an average measure of bias was computed, and the ANOVA repeated (now with only one factor: ISI). The repeated measure ANOVA revealed a main effect of ISI (after Greenhouse-Geisser corrected) $F(3.84, 88.20) = 4.136$, $p = 0.005$.

A Bonferroni corrected post-hoc analysis of the main effect of ISI revealed that the spatial bias was not significantly affected by modulations of cue-target interval[34].

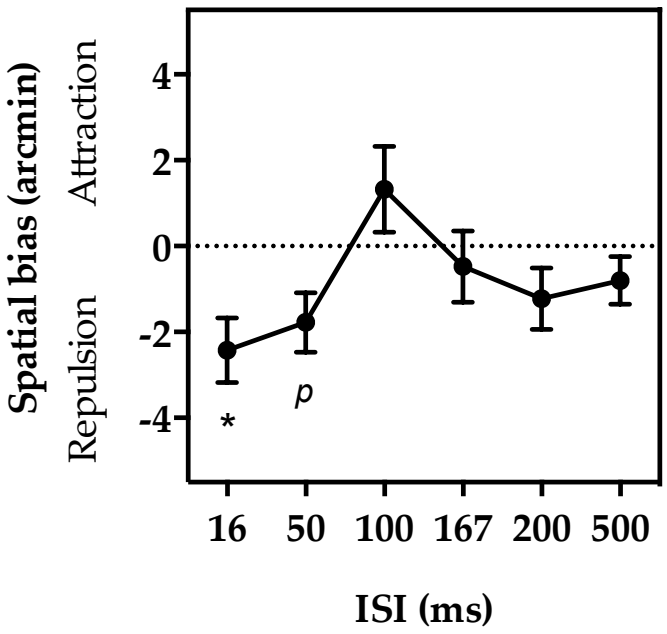

Figure 6-4 Average spatial bias across ISI of experiment 4 (VV). Asterisks represent a statistically significant departure from 0°. *p* represents a significant result at $\alpha = 0.02$ without bonferroni corrections. Error bars are SE.

Figure 6-4 shows the average bias across ISI. A one-sample t-test was used to confirm the departure from zero. Results were adjusted using the Holm-Bonferroni method (a less stringent method to the classical Bonferroni; Holm 1979), however, only ISI 16 ms was significantly different from zero, t(23) = -3.22, $p = 0.004$, as the second arranged *p-value* (50 ms; $p = 0.019$) was not significantly different from the adjusted *p-value* (0.05/5 = 0.01), thus stopping the remaining adjustments. A detailed description of this method can be found in the results section of experiment 1 (chapter four). Table 6-1 shows the averages, *p-values*

[34] However, ISI 16 ms (-2.46; SE 0.78) and 100 ms (1.32; SE 1.02) just missed significance p = 0.062; as well as ISI 50 ms (-1.74; SE 0.72) ISI 100 ms $p = 0.056$

and adjusted *p-values* across ISI. A further calculation of the effect size (ES) for ISI 16 and 50 ms revealed a large effect size of Cohen's d = 1.34 and d = 1.04, respectively. The reaming ISI (which were not significantly different than zero) show medium or weak ESs: d = 0.5 for 100 ms; d = 0.25 for 167 ms; d = 0.7 for 200 ms; and d = 0.63 for 500ms.

ISI (ms)	**Average bias (SE)**	***p* value**	**Adjusted alpha**	**ES cohen's d**
16	-2.4 (0.78)	0.004	0.008 *	1.34
50	-1.74 (0.72)	0.019	0.01	1.04
100	1.32 (1.02)	0.206	0.05	0.5
167	- 0.48 (0.84)	0.561	0.05	0.25
200	-1.2 (0.72)	0.105	0.05	0.7
500	-0.84 (0.54)	0.138	0.05	0.63

Table 6-1 Average bias and p-values of the one-sample t-test used to test the departure from zero. Adjusted alpha values correspond to Holm-Bonferroni correction. Only ISI 16 ms reports a significant repulsion. Asterisks represent significance.

6.2. EXPERIMENT 5 – THE AUDITORY ARE

6.2.1. **Introduction**

The behavioural benefits of directing attention to a region of space are well documented in the literature, but in sum, an object appearing at the attended location can be perceived faster and more accurately than an object appearing at unattended locations (Posner 1980; Posner and Cohen 1984; Posner and Petersen 1989). These effects were first reported in the visual modality, however they are not exclusive: the same attentional facilitation (faster and more accurate responses) are reported in tactile (Spence and McGlone 2001) and auditory modalities (Spence and Driver 1994). Furthermore, the processing of attended stimuli is characterised by an enhancement of neural responses within areas subserving the stimulated modality (Corbetta et al. 1990, 1993), but also by a mechanism that allows the suppression of task-
-irrelevant information (RF sharpening). This "amplification" of neural activity (often termed as "attentional gain", and reviewed in Posner and Dehaene 1994) and sharpening is observed in both auditory and visual modalities. Gain control is believed to serve the purpose of increasing the signal-to-noise ratio in the "attended" sensory pathways, when compared to the "unattended" pathways, and attentional mechanisms of sharpening and gain control have been observed in imaging studies of unimodal visual (fMRI; Murray and Wojciulik 2004) and auditory conditions (MEG; Okamoto et al. 2007). At the cell level, enhancements in the neuron's response rate and sharpening of RFs can be found when attention is directed towards a visual (see e.g. Spitzer et al. 1988) or an auditory stimulus (Fritz et al. 2007a, 2007b).

If attention behaves similarly in the auditory and visual modality, then it stands to reason that if the ARE is due to attentional mechanisms, it

can also be observable in the auditory domain. This notion can be further supported by studies showing that similar brain regions involved in visual spatial attention are also involved in auditory spatial attention (Hopfinger et al. 2000; Corbetta and Shulma 2002; Green and McDonald 2008; but see Green et al. 2011). Here we ask if the ARE is solely an effect of visual perception or can auditory perception incur in the same spatial errors as the visual ARE. The present experiment will re-adapt the unimodal visual ARE used in the previous experiment to study the existence of an exclusive unimodal auditory ARE.

6.2.2. **Methods of experiment 5: auditory ARE**

6.2.2.1. Participants

Thirty-one (31) volunteers gave consent to participate in this experiment (age range 19-44 years, mean of 23.32 years, mode of 22), however, after applying the exclusion criteria, only data from seven (7) participants were used in further statistical analysis. The exclusion of such high number of participants was further analysed and the results will be discussed in the results section. Participants were naïve to the purpose of the study and had normal hearing (confirmed by a five frequency pure tone audiometry) and normal or corrected to normal vision. Participants were tested individually and provided informed consent prior to inclusion in the experiment.

6.2.2.2. Materials

The same set-up used in the previous experiment was also used in this experiment. In summary, the materials used in this experiment comprised of a stimulating computer (that served as data acquisition unit as well), an infrared eye tracker with a dedicated computer (detailed description of its use can be found in the General Methods chapter, *section 2.2.1*), a chin rest, a computer screen, two speakers and a response box. Since this experiment attempted to test the visual ARE in unimodal auditory conditions the computer screen served to display a fixation dot because there is evidence eye movements influence auditory spatial perception (Razavi et al. 2007).

6.2.2.3. Stimuli

Stimuli consisted of an auditory cue and an auditory target (AA). The details of the AA pairing used in this experiment as well as the respective calibration procedures can be found in the General Methods

chapter (2). Succinctly, the auditory cue was a short BBN (33 ms duration) played randomly at one of three cue locations, each trial: left or right (±10°) and middle (0°), 6.4° above the centre of the screen. The auditory target (66 ms duration) was the top vertical line of a vernier display, which assumed (randomly each trial) 6 linearly spaced positions around 0°. The range of targets was piloted before in chapter four (see *section 4.1.2*) and was set as three linearly spaced positions at both sides of the middle (±7.5°, ±5°, ±2.5° and 0°). The stimuli described here is illustrated in figure 6-5, below

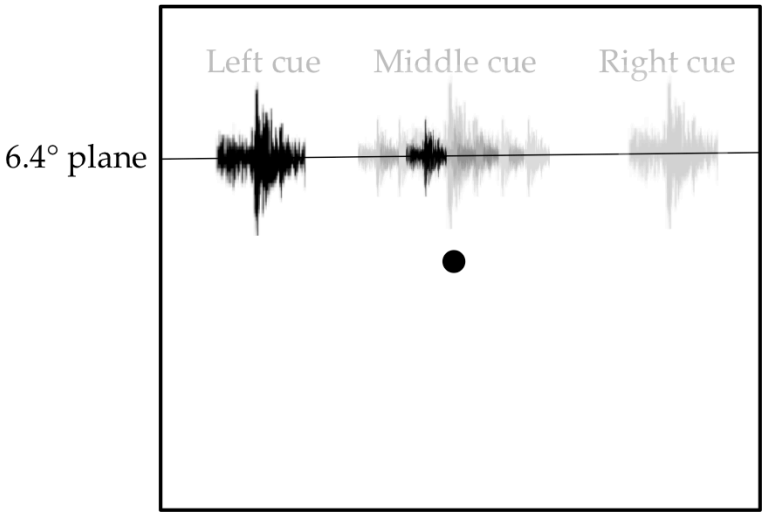

Figure 6-5 Relative positions of the auditory stimuli as seen by the participant with reference to the 6.4° plane, where the centre of the speaker cones were positioned.

6.2.2.4. Procedure

Procedure was similar to the previous experiment, with exception of the presented stimuli (auditory cue and target). Figure 6-6 illustrates the events contained in one trial of the present experiment. The procedure is similar to the one described in the previous experiment of the present chapter and in previous chapters 3 and 4, but, in summary, the participants completed a five frequency PTA to confirm normal hearing status. After consent was given the participants were accompanied to a sound proof room where the experiment was

explained: a fixation dot appeared at the centre of the screen, following which a sound preceded another sound. The task was to ignore the first sound and respond in a two alternative forced choice manner if the second sound came from the left or right.

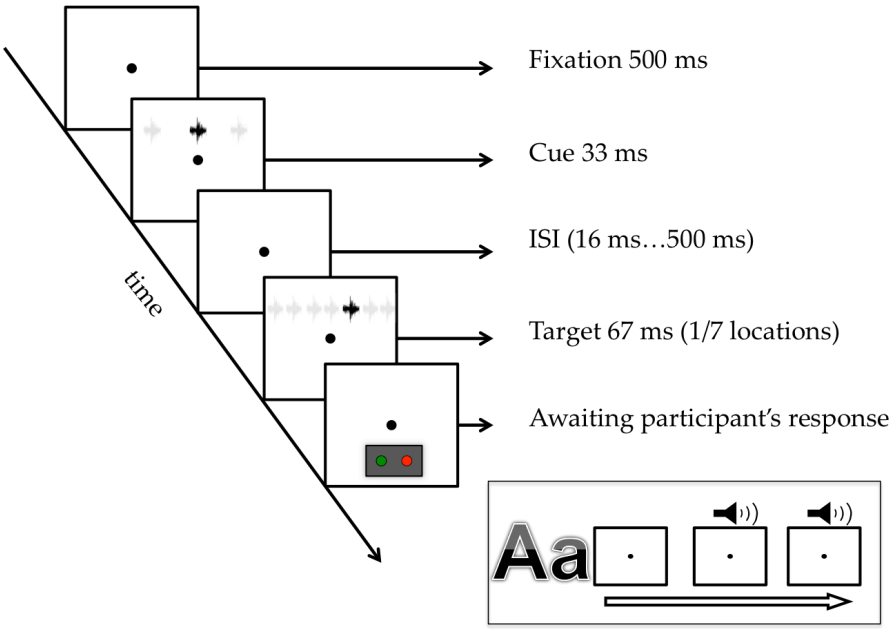

Figure 6-6 Events contained in one trial of the AA ARE. Bottom right is the visual card used to aid instructions to the participant.

After response was given by pressing the corresponding button (left or right button for left or right judgement) in the response box, another trial would start. Each participant completed 315 trials of 15 repeats of each cue/target combination (3 cue positions x 7 target positions x 15 repeats) in one single session. Participants completed six sessions, one for each ISI (16 ms, 50 ms, 100 ms, 167 ms, 200 ms and 500 ms). The order of the sessions was randomised for each participant. Due to the difficulty of the task, participants were allowed a maximum of one practice run comprising of two trials per target azimuth, in each condition, or until the tester was confident the participant understood the instructions. An infrared eye tracker was used in-
-situ to insure eye gaze was maintained in the fixation dot.

6.2.3. **Results of experiment 5: the auditory ARE**

The statistical analysis for this experiment followed the same general structure as the previous experiment (the basic visual ARE). In summary, a factorial ANOVA was used to investigate the main effects of ISI and cue symmetry, followed by post-hoc analysis to confirm the departure from zero (repulsion or attraction).

A Bonferroni corrected repeated measure ANOVA with 2 factors (bias side [2 levels] and ISI [6 levels]) revealed that there was no main effect of bias side, after Greenhouse-Geisser corrected, $F(1,6) = 0.20$, $p = 0.67$. In other words, the spatial bias is independent of cue side, thus, as before, an average measure of bias was computed. As such, the two bias were combined in a single quantitative measure of average bias.

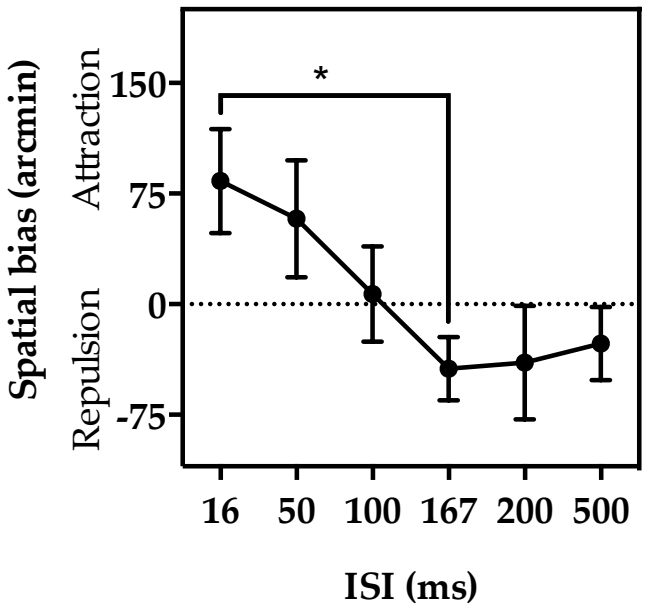

Figure 6-7 - Average spatial bias across ISI, experiment 5 (AA). Dashed line divides repulsion from attraction. Asterisks represents a significant difference in bias between ISI 16 and 167 ms, however none of the ISIs were significantly different from zero. Error bars are SE.

A further ANOVA with only ISI as the 6 level factor revealed a main effect of ISI, $F(3.28, 19.67) = 5.74$, $p = 0.005$. Post-hoc tests (Bonferroni corrected for multiple comparisons) revealed a weak but significant

difference between ISI 16 ms (M = 1.39, SE = 0.59) and ISI 167 ms (M = -0.73, SE = 0.36), $p = 0.047$, while the remaining ISI were not significantly different. Figure 6-7 summarises this interaction illustrating the average bias across ISIs. A one-
-sample t-test, used to confirm the attraction and repulsion for each ISI, did not reveal any significant attraction or repulsion, after corrections for multiple comparisons. Table 2 shows the results of the t-test across ISIs, with the adjusted (Bonferroni) alpha value. Step down methods for correcting for multiple comparisons, like the Holm-Bonferroni would not show any advantage because the first p value is already below the alpha threshold (0.008).

ISI (ms)	Average bias (SE)	*p* value	Adjusted alpha
16	1.39 (0.59)	0.056	0.008
50	0.96 (0.66)	0.195	0.008
100	0.12(0.54)	0.838	0.008
167	- 0.73 (0.36)	0.087	0.008
200	-0.66(0.64)	0.344	0.008
500	-0.45 (0.41)	0.321	0.008

Table 6-2 One-sample t-test results of bias against hypothetical zero, in order to confirm a repulsion or attraction.

Due to the large number of excluded participants (n = 24), data were re-
-analysed in order to try to "rescue" potentially beneficial data.

6.2.3.1. Analysis of excluded data

In appendix C6.2 the reader can find a reprint of figure 5-8, the pipeline of the general data analysis of this thesis. A crucial step in the pipeline is the fitting of NLRMs that will enable the estimation of the PSEs, used later in the statistical analysis. In the present experiment, after fitting

the NLRM and applying the exclusion criteria, only seven (7) participants were included in the statistical analysis.

Illustrated in figure 6-8 are 11 participants that were excluded from ISI 100 ms. Even though on average all the NLRM presented acceptable GOF R^2 values, indicating that the model was a good fit, some participants (such as S26 in the left cue condition or S1 and S14 in the right cue condition) had an estimated point of subjective equality (PSE) that was beyond the range of targets.

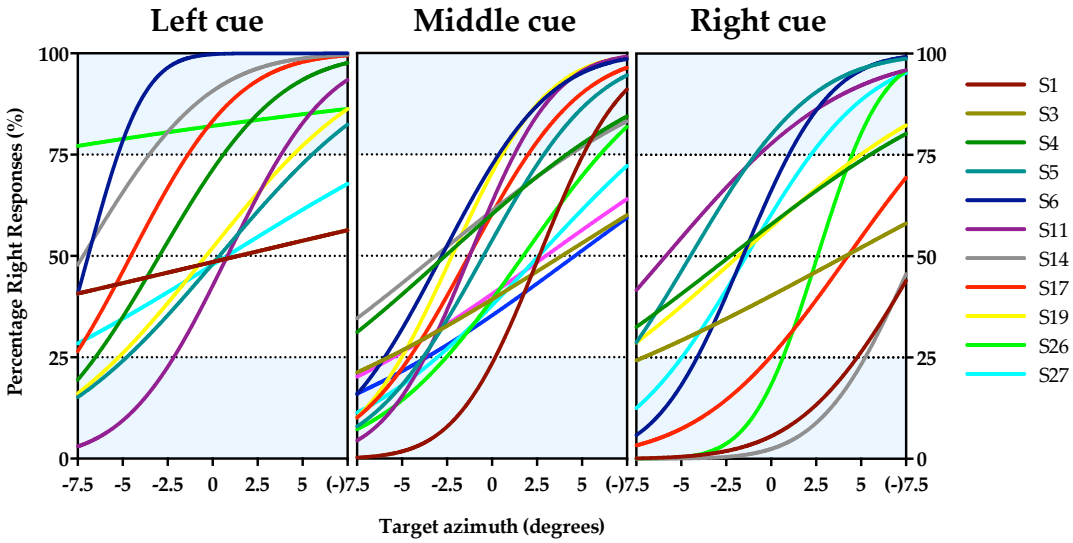

Figure 6-8 Excluded participants from ISI 100 ms. Some participants might have a good performance, especially in the middle cue condition, but if the fitting is bad in the other conditions the participant cannot be included in further data analysis. Subject 1 is S1, subject 26 is S26, etc.

Furthermore, all of the participants included in this figure fail to reach 75% of correct responses in at least one of the three cue conditions. Let us take participant S6 as an example (in dark blue). This participant shows a good psychometric fitting in the left and middle cue condition with performance just below 100%. However, in the right cue condition, the participant's performance worsened and the estimated PSE approximates 50% performance. Since all of the cues are essential for the bias computations and further statistical inferences, this participant

was excluded based on his/hers performance on the left cue condition. The PSE estimated from this cue was not a reliable measure of this participant's behaviour. This is due to the fact that the range of targets was too small for this participant and the NLRM are only detecting part of his/hers performance, and not the complete function. Another good example can be seen analysing the fittings for participant S17 (in red), in figure 6-8. This participant shows a good middle cue performance but only just fails to reach the 75% performance threshold when cues arrive from the sides. This is a clear example that the stimulus range should have been extended (even by as little as 2.5°).

Table 6-3 shows the exclusion/inclusion of the first 8 participants in relation to the 6 ISIs, with crosses marking in which ISI the participant was excluded. The complete table is included in the appendix C.6 for the reader's review.

	16 ms	50 ms	100 ms	167 ms	200 ms	500 ms
S1			✖	✖	✖	
S2					✖	
S3	✖	✖	✖	✖	✖	
S4	✖	✖	✖	✖	✖	✖
S5	✖	✖	✖	✖		
S6		✖	✖		✖	✖
S7						
S8	✖					

Table 6-3 Sample of participants indicating the inclusion/exclusion for further analysis, per ISI. Green lines represent included participants; yellow lines included excluded participants in one ISI only. S1 is subject 1; S2 is subject 2 and so forth.

In green we have participant 7, which was one of the included participants in the statistical analysis. The yellow rows represent those participants that failed to be included in further analysis, but that were excluded because they missed one ISI only. Data from these

participants were further analysed to check if the exclusion criteria could be relaxed (particularly the third criterion: the estimated model must reach at least 75% performance at both extremes of the function; *section 3.3.5*) to include them, thus increasing the sample size. Consulting appendix 1 of the present chapter, the reader is able to note that the participants in the shaded yellow rows are: S2, S8, S13, S22, S23, S24, S25, S29 and S31. All the other participants were excluded from two or more ISI conditions and were not considered. Data from these participants was grouped according to ISI. Figure 6-9 depicts the two participants that were excluded from ISI 16 ms (S8 and S31).

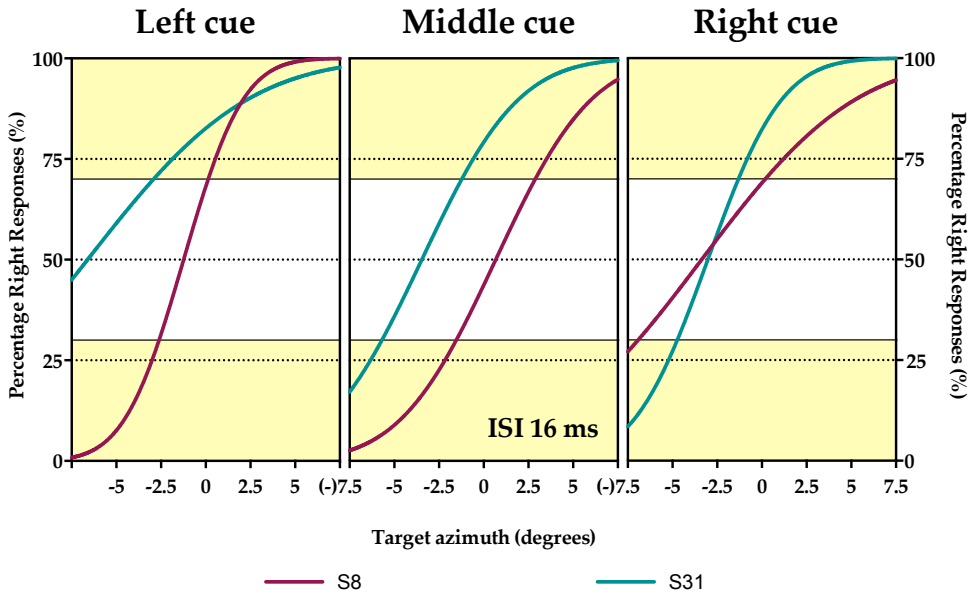

Figure 6-9 NLRM fitting for the excluded participants of ISI 16 ms (S8 and S31). Shaded yellow areas are now a relaxed threshold of performance at 70% of correct responses.

By applying a more relaxed performance threshold at 70% (yellow areas), it is possible to include participant S8 in further analysis, since the right cue is now below threshold. Data from the remaining participants can be seen in appendix 3, but overall, S8, S23 and S4 were the only participants to be added to the initial seven (7) participants, making a total of 10 participants. Data was reanalysed in SPSS in the same approach as before, but with the revised sample.

The first ANOVA, did not reveal any effects of cue side, $F(1, 9) = 0.80$, $p = 0.783$, and the second ANOVA (now with one factor: ISI) revealed a main effect of ISI, $F(3.34, 30.1) = 6.45$, $p = 0.001$. Post-hoc tests (Bonferroni corrected) revealed a main difference of ISI 16 ms (M = 1.171; SE = 0.45) and ISI 200 ms (M = -1.01; SE = 0.48), $p = 0.024$, but none of the ISI showed a statistical significant bias, as revealed by the one-sample t-test. This means, that there was no significant attraction or repulsion detected. Table 4 shows this result and additionally it shows the significance values for the t-test with the original sample size (n=7). As can be seen, adding a further 3 participants did not change the overall results: there was not a significant repulsion or attraction of auditory targets when lead by auditory cues. These results were compared to an adjusted alpha using the Bonferroni correction, which is known for its stringency (here, using step down methods could not improve the significance rate since first *p-value* in the order [16 ms; $p = 0.024$] was greater than 0.008 [= 0.05/5]).

ISI (ms)	**N = 7**		**N = 10**		**Adjusted α**
	Mean bias (SE)	***sig***	**Mean bias (SE)**	***sig***	
16	1.39 (0.59)	0.056	1.17 (0.45)	0.029	0.008
50	0.96 (0.66)	0.195	0.69 (0.60)	0.281	0.008
100	0.12 (0.54)	0.838	-0.15 (0.44)	0.745	0.008
167	- 0.73 (0.36)	0.087	-0.38 (0.41)	0.377	0.008
200	-0.66 (0.64)	0.344	-1.01 (0.48)	0.067	0.008
500	-0.45 (0.41)	0.321	-0.40 (0.40)	0.348	0.008

Table 6-4 Comparison of the one-sample t-test between the initial sample of 7 participants and the updated sample of 10 participants.

6.3. INTERIM DISCUSSION OF CHAPTER 6

The ARE has been almost exclusively studied in the visual domain and not many studies investigated this effect with auditory targets. Thus, the present chapter aimed to replicate the original ARE effect in a first experiment and to investigate if this effect is also found in the auditory domain (in a second experiment). The present interim discussion will follow the same order and it is divided into two sections; one devoted to summarising and discussing the visual ARE (experiment 4) and another aimed at the auditory ARE (experiment 5).

6.3.1. Discussing the results of experiment 4 – Visual ARE

The general aim of experiment 4 (visual ARE) was to modify the cue/target paradigm developed in previous chapters to reproduce the basic ARE reported by Suzuki and Cavanagh (1997). Currently there is not an established method used to evoked the ARE, whether it is in its unimodal or crossmodal form, thus, this experiment served to test if the paradigm used successfully in the crossmodal ARE experiment (chapter 4) can also serve to evoke the basic unimodal visual effect.

The results show a significant repulsion at 16 ms of cue-target interval and at 50 ms. Moreover, this repulsion presented a large effect sizes for both ISIs (d = 1.34 and d = 1.04, respectively). The usefulness of the effect size index is that it is independent of the sample size. Furthermore, the spatial bias was independent of cue positions, as it was elicited in equal sizes by the left and right cue. Nevertheless, the basic visual ARE observed by Suzuki and Cavanagh (1997) could only be reproduced here, with confidence, for short ISIs. The results of our unimodal visual ARE experiment do not agree fully with the original ARE study of

Suzuki and Cavanagh (1997). The authors report a repulsion of 9 arcmin while the present results suggest 2.5 arcmin. Moreover, the original ARE was shown to be significantly above zero when the cue and target were presented simultaneously, and would continue to rise until it peaks at around 200 ms of interval between cue and target. After this, the ARE decreased and stabilized in a steady state, however, it never fully disappeared. On the other hand, we have shown that after 16 ms the ARE decreased and disappearing unequivocally at 100 ms and thereafter. These results also contrast to those from Arnott and Goodale (2006) that show a strong ARE at 100 ms but fail to show any main effect of ISI. One thing to note is that my results were Bonferroni corrected to six comparisons. Considering that some statisticians recommend avoiding corrections for a few comparisons only (Rothman 1990), the significance of the effects would change as the *p-value* for the ISI 50 ms would be reported as a significant repulsion, if no corrections would have been performed. Nevertheless, the present experiment still shows that the ARE is resolved by 100 ms ISI, which contrasts with the Arnott and Goodale (2006) study. Here methodological differences could have played a significant part. The study by Arnott and Goodale used a single cue paradigm, like the present experiment, however, the authors report a left cue repulsion and not a quantifiable measure of bias, since the middle and the right cue did not differ and since the authors did not use these cues to create a context with the left cue. As said in the previous chapter four, a left cue repulsion of (for example) 10 arcmin is meaningless unless compared with both a middle or a right cue. If the middle cue presents a repulsion of 9 arcmin and the right cue presents a repulsion of 8 arcmin, then, the size of the ARE if of 1 arcmin, not 10 arcmin. Furthermore, as the ANOVA performed by the authors did not reveal any effects of ISI, they combined both ISIs, thus these

results pertain the 50 ms and the 100 ms conditions added together. But, this contradicts both the original ARE study (that found the ISI to have an effect up to 200 ms) and the present experiment. Furthermore, as observed in the previous chapters, several mechanisms may operate at several cue-target intervals, thus, adding both ISIs in a single analysis might mask different results.

Direct comparisons between the present thesis and the original study can be misleading largely due to methodological differences. For instance, our measure of the ARE is an average of two cue positions, while Suzuki and Cavanagh took the bias value given by one cue location. Furthermore, the authors used a dual cue paradigm, in the original ARE study, where two cues were simultaneously flashed in diagonally opposite quadrants. In a pilot, the authors observed that the ARE was larger using a two-cue paradigm, instead of presenting a single cue at one of the two hemifields. Additionally, the participant was seated 60 cm away from the screen, in the original 1997 ARE study, though, this distance was 45 cm in the present experiment. In the pilot of the 1997 study, the participant was seated 46 cm from the screen, but the authors increased this distance to "60 cm, from the monitor such that each pixel subtended 2.1'" (Suzuki and Cavanagh 1997, p. 445). The authors used the longer viewing distance in the main experiments "to increase the resolution of the vernier offset drawn on the monitor" (Suzuki and Cavanagh 1997, p. 445). Moreover, the brightness of the masking squares in the original study was increased from 9.1 cd/m^2 in their pilot to 53.5 cd/m^2 to make sure the vernier targets were further disrupted after their presentation. The masking squares in the present experiment had a brightness of 13.7 cd/m^2 thus it is possible that fainter masking could have contributed to a fewer spatial errors, thus a smaller

ARE. It is unclear if the presence of a fixation symbol displayed through the entire trial might help participants judge the top vernier line as the ARE has been shown with (Suzuki and Cavanagh 1997; Arnott and Goodale 2006) and without (Pratt and Turk-Browne 2003; DiGiacomo and Pratt 2012) it during the targets display. The fixation dot/cross could work as an anchor and it is plausible that some participants judge the top vernier line in relation to the middle of the screen (as represented by the fixation dot) and not in relation to the bottom vernier line, despite instructions. One way to control for this would be to remove the fixation dot/cross but further research needs to address these methodological concerns. Resolving the differences between paradigms would further inform about the ARE's sensitivity to task manipulations.

6.3.2. Discussing the results of experiment 5 – Auditory ARE

Experiment 5 investigated whether the visual ARE (also shown across modalities in chapter 4) can occur in unimodal conditions of auditory stimulation. The ARE in the visual modality is characterised by a misperception of space in the loci of interest (the foveated location) when attention is directed to an irrelevant location. This mislocalization is shown in a cue-leading paradigm when the first stimulus (the cue) disrupts (repulses) the perception of a subsequent target. Here I investigate if the less spatially accurate auditory system (when compared to the visual system) is capable of such small errors of attention.

The results show an attraction at very small ISIs that tends to zero or negative values (repulsion), which can be seen in picture 5-7. This notion is further encouraged by a significant difference between ISI 16

and 167 ms, however, the results seem too noisy to draw firm conclusions. None of the ISIs were reported as achieving statistical significance and as such there is not enough evidence to reject the null hypothesis, that there is no difference between the induced bias and no bias (the hypothetical zero of the t-test). One vital aspect of this experiment that needs to be addressed in this discussion is the participant exclusion rate. As can be seen in the results section, 31 participants volunteered for this experiment, however, only seven (and later, after reanalysing and modifying the exclusion criteria, ten participants) were included in further statistical analysis. The reason for such high number of participants that failed the inclusion/exclusion criteria is due to the fact that the difficulty of the task was not adjusted to the sample population. In other words, the range of targets used in this experiment did not allow participants to reach 100% correct responses (or near). The present experiment used targets that had previously been piloted in chapter 3 and were shown to be adequate to naïve individuals, untrained in spatial tasks, however, this stimulus set was clearly inadequate in the present experiment. Going back to the pilot experiment, it can be seen that the major difference between the pilot (and also the main experiments 1 and 2, which show adequate range of targets) and the present experiment is in the nature of the stimuli that preceded the targets. The pilot experiment in chapter 3 was conducted in crossmodal conditions (a visual cue preceded an auditory target), but in the present chapter, an auditory cue preceded a target of the same modality. Studies on divided attention were able to show that selection of information is harder within modalities. Reese and colleagues (2001) showed that attention capacity is restricted within-modality (in their case, auditory modality) but not between-modality (visual-auditory). The authors speculated that the processing of visual

stimulus (whether or not it is task or modality irrelevant) could occur whenever there is visual capacity to process them and that this process is independent of the auditory load resources. The fact that our experiment used within-modality stimuli created a harder task than if across-modality stimuli had been used. It is plausible that in the present experiment the observers had to distribute auditory processing resources to the cue (led by the exogenous nature of the attention leading cue) and immediately after, to the target (necessary by the nature of the task that required a voluntary answer). This scattered allocation of attention could have induced a processing load in this experiment that is different than the load required by the crossmodal task of chapter 4, thus, the range of targets here was simply harder to perceive. In future experiments, range of spatial targets should be tested under the specific conditions of unimodal and crossmodal loads that the experiment requires.

In summary, I did not find an auditory ARE. In line with this result seems to be the current literature on the visual ARE. For example, DiGiacomo and Pratt (2012) measured the effect in both monocularly and binocularly conditions and showed that the use of one eye only did not compromise the ARE, which suggests there was no need for binocular visual processing to be present. Thus, it is possible that the ARE derives from the monocular receptive fields of cells somewhere before V1 (the first stage of the visual system where cells are tuned to binocular differences). Moreover, in support of this notion, Pratt and Turk-Browne (2003) showed that the ARE perception and also action, thus, to affect both perception and action, it must be carried down both visual pathways and the authors suggested that the effect originates

relatively early in visual processing, arguing that it must be instantiated before the visual signal segregates into their ventral and dorsal streams.

Furthermore, due to the temporal and spatial dependency of the effect and due to different ways both modalities build a spatial percept (auditory modality being more computationally complex and less spatially accurate) it is unlikely that the auditory modality is able to generate such effect.

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CHAPTER 7 ATTENTION IN ADAPTATION

7.1. INTRODUCTION

The present chapter derives from a question raised in section 2.4.6 of chapter two, the review of literature. In this section I make the point that attention and sensory adaptation are traditionally studied in isolation, and that seldom is the case where studies investigate the combined effects of attention and sensory adaptation. Combining this with the fact that most psychophysics paradigms (such as the ARE), repeat the same stimuli thousands of times, uninterruptedly, one could hypothesise that sensory adaptation could be further a contributor to the ARE.

The present experiment will modify a spatial adaptation paradigm that uses the mean and standard deviation measures of statistical dispersion to investigate the effects of auditory attention in auditory adaptation. Dahmen and colleagues (2010) investigated how spatial processing in the auditory modality adapts to variations of environmental statistics. Human listeners were presented with a 1s long adaptation stimulus immediately followed by a 100 ms static stimulus. Participants indicated by button presses on a keyboard, if the static stimulus was perceived in the right or left of the midline. In the adaptation period the interaural level difference (ILD) was randomly drawn every 5ms from one of 6 Gaussian distributions (1 – baseline distribution with mean 0dB and SD 20dB; 2 – mean -15dB and SD 20dB; 3 – mean +15dB and SD 20dB; 4 – mean 0dB and SD 5dB; 5 – mean 0dB and SD 10dB; 6 – mean 0dB and SD 15dB). Each participant was tested with a total of 7 different static ILDs. To clarify the above, the mean of the overall distribution (from where the individual ILDs were drawn) varies the

perceived laterality of the stimulus, while the variance changes the spatial sensitivity. Thus, for example, changing the mean shifts the range of possible positions to the left or right and changing the variance widens or narrows the location of possible positions. Zero ILD meant the level was equal in both ears, with negative values meaning that the level was higher in the left ear. Figure 7-1 depicts Dahmen's stimuli design, with examples of a distribution that would have been perceived coming from the centre (in black), the left (in green) and the right (in red). The distribution in blue would have been perceived as rushing sound more focused in one location, as the variance was decreased by half (when compared to the other three distributions):

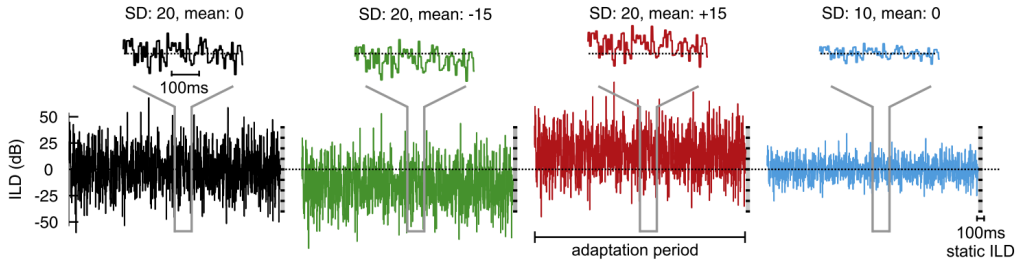

Figure 7-1 Figure from Dahmen et al (2010) showing the stimuli design. Licensed from Creative Commons Attribution License (CC BY).

The authors observed that by changing the mean of the overall distribution, participants would report significant shifts in the perceived position of the target, in the opposite direction to the adapter. Changing the variance would impact target discrimination, with smaller variances associated with steeper psychometric curves. A simplified version of this paradigm (two means and one variance) was piloted[35] in two participants (one auditory scientist naïve to the purpose of this study and the author of this thesis) in the free field, with similar results being observed: a repulsion of targets to the opposite side. One

[35] Piloted stimuli were the same as used in this experiment and thus is described in the methods section of this chapter.

aspect of the above-mentioned study that is relevant to this thesis is the fact that Dahmen did not specify where in space attention should be directed. Considering that Dahmen and colleagues (2010) investigated the effects of adaptation on spatial perception in a highly similar paradigm than the one used in experiment 5 of the previous chapter (six; auditory cue + auditory target), a Dahmen-like paradigm was adapted to be presented through the same set-up as used in past experiments of this thesis and to have additional attentional instructions. This is aimed at investigating if attention will facilitate or supress sensory adaptation.

7.2. EXPERIMENT 6 - AUDITORY ATTENTION IN ADAPTATION (AIA)

7.2.1. Methods

7.2.1.1. Participants

Nine paid participants (6 males) with age ranging from 20 years to 33 (mean age of 25.428 years, SD = 5.318) gave consent to participate in this experiment. Participants had normal hearing as confirmed by a five--frequency pure-tone audiometry (PTA) and were unaware of the purpose of the study. Two participants did not complete the data collection and where excluded from the study.

7.2.1.2. Materials

This experiment took place in the same acoustically treated room as the previous experiments and used the same setup to generate and present the stimuli.

7.2.1.3. Stimuli

Stimuli were generated using custom routines in Matlab (MATLAB 7.9, The MathWorks Inc., Natick, MA, 2000) and controlled using the Psychophysics Toolbox Version 3 (PTB-3) extension (Brainard 1997; Pelli 1997). Stimuli consisted of sounds presented through two speakers at a confortable listening level of 70 dB(SPL). The adaptation stimuli were two 1000 ms broadband noise (of 1000 Hz with a 3 ms $\cos^2$ ramp) with centre frequencies at 500 and 4000 Hz, filtered with a Butterworth octave-band filter of the 8^{th} order. The adapter consisted of individual noise bursts draw randomly every 5 ms (1 ms cosine square ramp) from one of two normal distributions: left (with mean of -15 dB and standard deviation of 10 dB); and right (with mean of 15dB and standard

deviations of 10 dB). Stimuli were generate with a sampling rate of 44100. The test stimuli were one of two (randomly selected each trial) 100 ms BBN (with a 5 ms $\cos^2$ ramp) with the same filter design as the adapter stimuli, centred at 500 and 4000 Hz. Both high and low frequency tests were seven BBN spaced between -7.5 (left) and 7.5 (right) dB ILD with a step size of 2.5. To control for attention deployment, an amplitude modulation signal (AM) was applied to the adapter (carrier). The modulating input signal was a 5 Hz sinusoidal with a 3 dB modulation index.

7.2.1.4. Procedure

The experiments setup used in the previous experiments was used in this experiment. Participants sat down in a sound treated room and rested their head on a chin rest located 45 cm away from the computer screen. Each trial began with an arrow indicated which adapter the participant should covertly direct attention to. This arrow was implemented as the attention control condition. An upward pointing arrow indicated that the participant should attend to the high frequency adapter and a downward pointing arrow indicated that the participant should attend to the low frequency adapter. After 500 ms (or 3000 ms in case it was the first trial of the block), two adapters were played (a low frequency and a high frequency) simultaneously, randomly picked from two spatial conditions: a low frequency adapter presented at the left with a high frequency adapter presented at the right (LL+HR condition) or a high frequency adapter presented at the left with a low frequency adapter presented at the right (HL+LR condition). After a 100 ms interval a 100 ms test sound was played. The test sound was randomly picked from 7 positions (-7.5 to 7.5 dB) and from two pitch conditions (low frequency or high frequency). Participants were told to

fixate on the tip of the arrow (displayed at the centre of the screen) and to attend to the instructed adapter (high pitch for upward arrow and low pitch for downward arrow) without making any saccadic movements. Participants were required to answer in a two-alternative forced choice (2AFC) manner if they detected a fluctuation in the adapter sound and if the second sound came from the right or left. The events of a single trial are depicted in figure 7-2. The responses were prompted by white text displayed instead of the arrow, at the centre of the screen: "Left or right?" prompted the answer to the perceived position of the test ILD; and " Fluctuation present?" prompted the answer to the perceived presence of amplitude modulation.

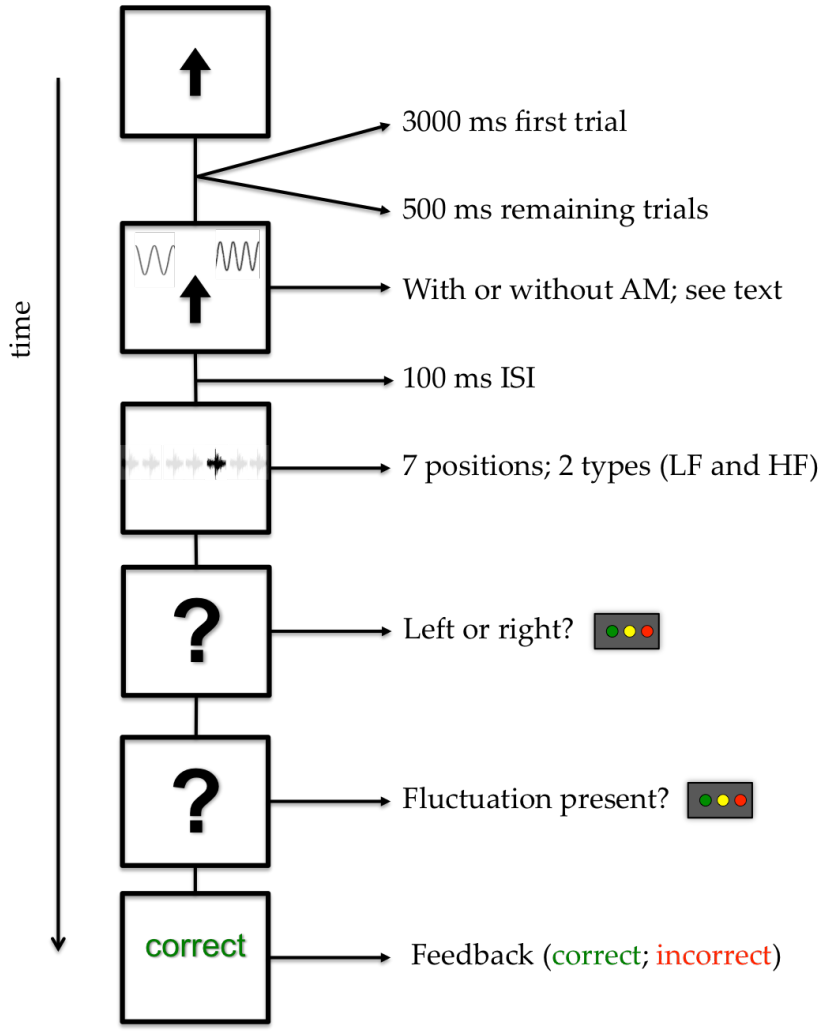

Figure 7-2 Events constituting one trial of the unimodal auditory attention in adaptation experiment (6).

Answers were given via the same response box used in the previous chapters: left button for left targets and right button for right targets, however, in the case of the amplitude modulation detection, the left and right button served as "no" and the middle button served as "yes". To control for attention deployment to the adapter, both attended and unattended adapters contained an amplitude modulation in certain trials. The amplitude modulation appeared in the attended adapter with a probability of 0.3, and it appeared in the unattended adapter with a probability of 0.15. If the participant detected the presence of the modulation in the attended adapter and not in the unattended adapter, this would be indicative that the participant was indeed directing attention as instructed by the arrow. The arrow remained in the centre of the screen until after the test ILDs. After the response to the second question ("Fluctuation present?") a feedback text appeared in the centre of the screen indicating if the participant had detected the presence of the modulation in the adapter. The "correct" and "incorrect" displayed text appeared in green and red, respectively. Each participant completed 15 repeats for all the conditions: 1- Adapters spatial condition (×2): LL+HR and HL+LR; 2- Attention condition (×2): attend to low frequency and attend to high frequency; 3- Target frequency (×2): low and high frequency; 4- Target position (×7): left (-7.5, -5, -2.5), middle (0), right (2.5, 5, 7.5); Total = 15×7×2×2×2 = 840 trials.

The experiment was broken down into six (6) blocks (runs) of approximately 20 min each run (depending on the speed of response) to avoid fatigue. The attention condition was randomised only per run so that in each block the arrow was always the same. In other words, the attention to the high or low frequency adapter would only change with the next block. Participants had a 5 min rest between blocks.

Two participants completed the six blocks in separate days (1 block per day), while the rest completed the full experiment in two or less sessions.

7.2.2. **Results**

The proportion of right responses was calculated for both target conditions (low and high frequency targets). Figure 7-3 depicts the average responses across all conditions.

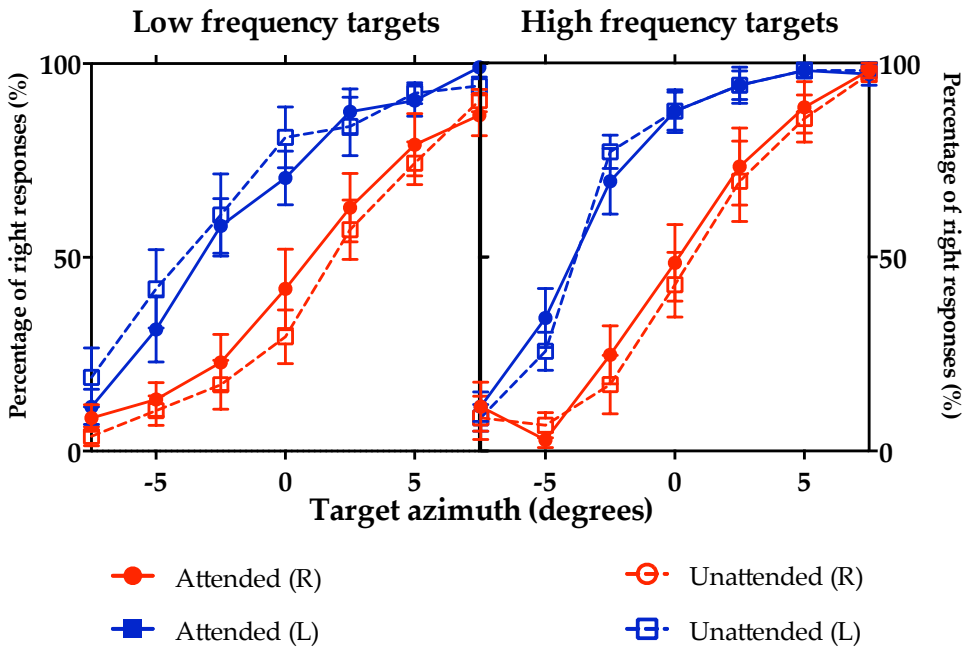

Figure 7-3 Average data from experiment 6 grouped into low (plot on the right) and high frequency targets (plot on the left).

The solid lines represent the responses where the participant was attending to the same adapter as the target (low frequency in the case of the left graphic and high frequency at the graph on the right), with the colours indicating the location where the adapter was presented (blue for left and red for right). The solid blue line in the left graph represents the responses to trials where the participant was attending to a left low frequency target. Conversely, dashed lines represent the responses where the participant is attending to an adapter of different frequency

as the target. For example, the dashed red line, depicted in the right graph, represents the trials where the participant was attending to a right low frequency adapter. PSEs were individually extracted according to the General methods chapter (chapter 3) and imported into SPSS for statistical analysis. Figure 7-4 illustrates the NLRM fitted to a representative participant. The same colour scheme used in the previous figure was applied here, thus, to examine the fitting of low frequency responses when attending to a high frequency target that was presented at the left, the reader is directed to the blue dashed line in the left graph.

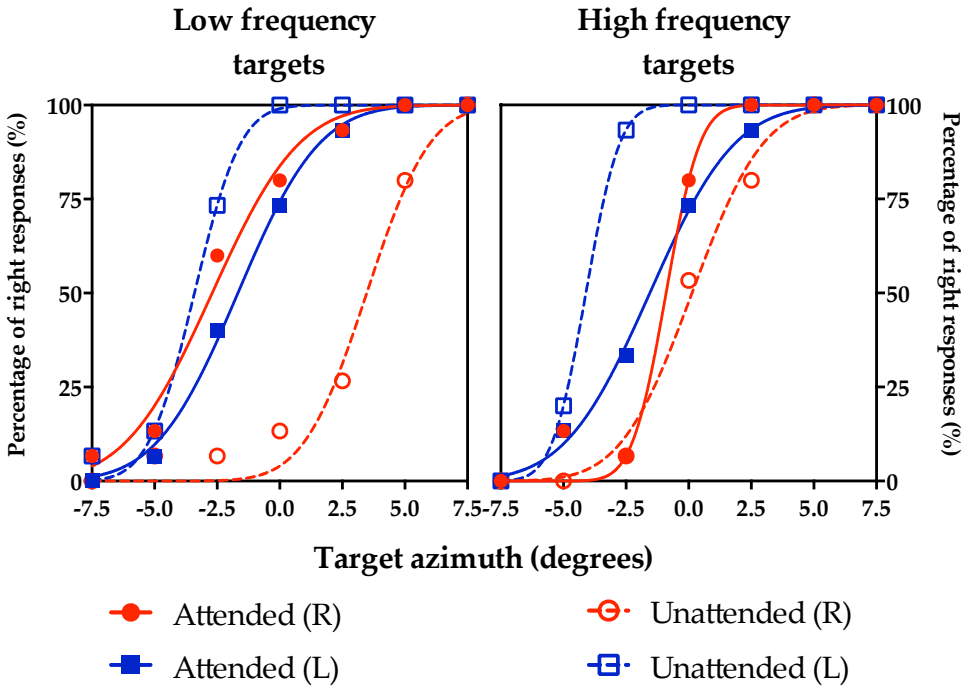

Figure 7-4 Data from representative participant of experiment 6, fitted with the NLRM described in section 2.3.3 of the General methods chapter.

A repeated measures ANOVA with 3 factors, each containing two levels (attention condition [attended and unattended]; target frequency [low and high frequency]; and adapter location [right or left]) was used to investigate the effects of attending to an auditory adapter on the lateral perception of an auditory target. The main effects of frequency

(F[1,6] = 1.14, p = 0.326) and attention (F[1,6] = 0.16, p = 0.902) were reported as not significant. There was a main effect of location indicating a perceptual bias on right adapters that differ from left adapters, F(1,6) = 71.5, p < 0.000. No significant interactions were reported. The above statistics were corrected with Bonferroni and Green-Houser. The results from low and high frequency targets were averaged and a post-hoc paired samples T-test was used to compare the differences between attended adapter locations.

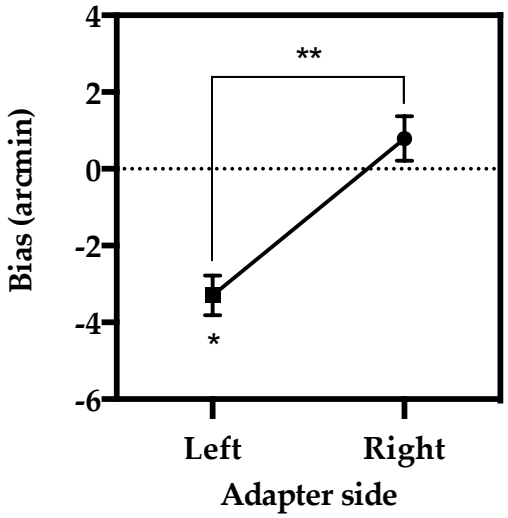

Figure 7-5 Bias induced by presenting an auditory adapter to the left and to the right. One asterisk represents a significant departure from zero. Two asterisks represent significantly different left and right bias.

A left adapter (M = -3.3; SD = 1.4) induced a significantly different bias when compared with a right adapter (M = 0.8; SD = 1.5), t(6) = -4.86, p = 0.003. A further one-sample t-test revealed a significant repulsion for the left adapter, t(6) = -6.36, p = 0.001, but not for the right adapter, t(6) = 1.36, p = 0.221. These results are illustrated in figure 7-5.

An intriguing result from the original ANOVA was the non-significant effect of frequency, which suggested that adapter bias is independent of frequency. To investigate this further, a paired-samples t-test was used to compare the bias across frequency and sides of the adapter-target

combinations: **pair 1** (Left LF adapter with Right HF target *versus* Left HF adapter with Right LF target); **pair 2** (Right LF adapter with Left HF target *versus* Right HF adapter with Left LF target). The results confirmed the general ANOVA: no differences were found for right, $T(6) = 1.065$, $p = 0.328$, and left targets, $T(6) = -0.01$, $p = 0.993$, across frequency. In other words, left (or right) adapters produced the same bias to right (or left) targets independent of the stimuli pair's frequency.

The attention deployment was investigated further using d prime measures. In this experiment, the participant was presented with trials where the adapter contained an amplitude modulation (valid-cue trials), but also trials where the modulation was present in the unattended adapter (invalid-cue trials). The participant was asked to attend to an adapter but was asked to respond in a 2-alternative forced choice manner if he detected the presence of a fluctuation (regardless of the side of the fluctuation). Moreover, the participant was informed that the fluctuation had higher probability of appearing at attended locations, and thus, he would perform better if attending where instructed each trial. The purpose of this was to control for attention deployment, with the premise that a fluctuation would be identified with more accuracy at attended locations, than at unattended locations.

The analysis of the AM task was framed around attended location as this was the underlying theme of the thesis. The AM detection task is a control for attention deployment designed to determine if the participants were attending to the designated location, instructed during the experiment. However, the hypothesis in question for this experiment is related to the lateral bias promoted (or not) by the previous sensory adaptation. For this reason, the graphical outputs will be generated with "attended location" in mind.

To measure this discriminability a statistic (d prime; or d') based on signal detection theory (STD) was implemented. Whenever a participant pressed the middle button, a response was registered, related to the perception of the AM. This was coded as a "Hit". Hits at attended locations that contained the AM were coded as "valid" trials; hits at unattended modulated locations were coded as "invalid" trials and trials where there was no modulation were coded as "false alarm". D prime was defined as the difference between the z-transformed probabilities of hits and false alarms:

$$\boldsymbol{d' = z(H) - z(F)}$$

Small d' values indicate that the participant had a poor discriminability. For example, a d' value of 0 indicates that the participant in unable to distinguish the two signals, and performance is at chance level.

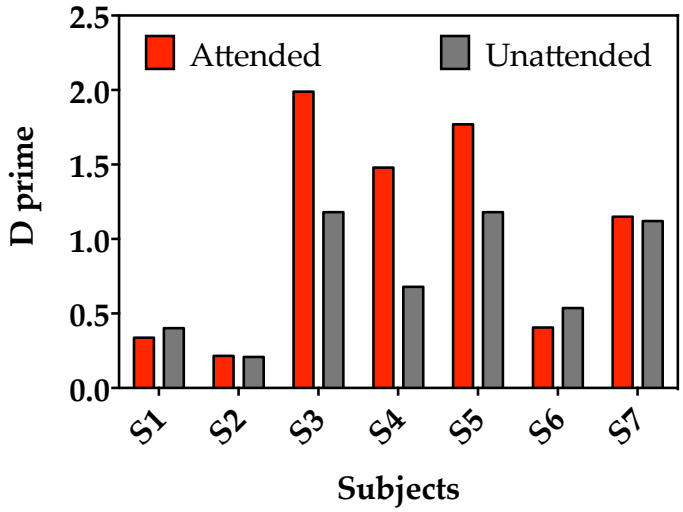

Figure 7-6 Probe (amplitude modulation) detection index (d') plotted for each participant.

While d' values can vary from -∞ to +∞ (see Stanislaw and Todorov 1999), it is more relevant in the present case to compare both d' values. By comparing the d' from valid trials with the d' from invalid trials we are determining to which extent attention deployment was controlled in the experiment. D prime was calculated for valid and invalid trials.

Figure 7-6 illustrates the d' values for individual participants. If we take subject 1 (S1) as an example, this subject had a small d' for attended locations, but more importantly, this value was very close to the d' at unattended locations. This meant that the discrimination performance of this participant at attended locations was identical to that at unattended locations. Conversely, participants 3, 4 and 5 show a larger d' value at attended locations when compared to d' values at unattended locations. These participants were able to respond more accurately to the AM probe at attended locations. The average d' values for both attention conditions were calculated. A repeated measures ANOVA with two levels (attended and unattended) was used to compare the d' values. The d' at attended location (M = 1.05; SD = 0.37) was reported as not significantly different from the d' at unattended locations (M = 0.76; SD = 0.40), $F(1, 6) = 3.35$, $p = 0.117$. This relationship is illustrated in figure 7-7:

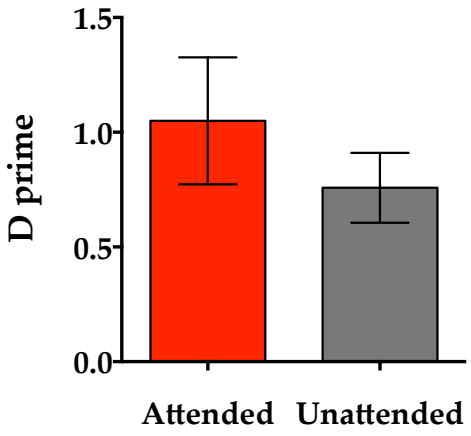

Figure 7-7 Average d' values for the attended and unattended locations.

7.2.3. **Interim discussion of experiment 6**

The aim of the present experiment was to test if spatial adaptation is modulated by attention. A secondary aim was to extend the Dahmen et al (2010) study by adapting the paradigm to free field and include measures to control for the allocation of attentive efforts. The results do not show a main effect of frequency and attention, with a repulsion being observed for the left adapter only, while the right adapter did not differ significantly from zero. When analysing the ability of the participants to discriminate between the AM at attended and unattended locations, no differences were found, indicating that the measure used to control for attention allocation (the AM detection task) was of poor reliability. The present experiment was successful in replicating part of the Dahmen et al (2010) behavioural study by showing a clear repulsion effect. Furthermore, the present experiment was also successful in adapting the Dahmen et al paradigm to free field, expanding the options of this method in future studies of auditory adaptation.

The pattern of results seems to follow the trend for spatial repulsion seen in the previous chapters. This is also in accordance with the results presented by Dahmen and colleagues (2010), however, the main question of this experiment was whether attention could modulate the effects of adaptation. For this it was essential to control for spatial attention, done here with an AM probe. However, the attention control did not work as intended and as such it was not possible to prove or disprove the null hypothesis (H0). When looking at the d' scores, it is noticeable that out of the seven participants, three show scores lower than 0.5 (S1, S2 and S6), and a further participant shows a d' a score very near 1 (S7). Taking into account that a d' at chance level is

characterised by similar scores for hits and false alarm rates, which yields a score of zero or near, it is worrying that almost half of the sample presents d' scores that are very close to chance level. This is indicative of the difficulty of the amplitude modulation detection task. It is not known if the low discriminability in detecting the AM is related to the AM detection task itself (in which case for some participants the sound fluctuation may have been presented below threshold of detection) or related to the fact that the participants can't satisfactorily direct their attention based on the frequency of the two adapters (or in other words, despite the instructions, the participant could still not understand the task). Furthermore, the presence of the red negative feedback could have made the participant covertly search elsewhere to receive a positive feedback. It is possible that the participant was attending to the instructed location, but also simultaneously attending to the opposite side in a case of divided attention, thus effectively dispersing attention to various locations, which has been proven to decrease cognitive resources (e.g. Johnson and Zatorre 2005, 2006).

It is necessary, in further experiments, to improve the attention probe discriminability (here represented with d' measures). Participants were trained in the probe detection task with the AM rising from 10 dB above background noise, to 6 dB and then finally to 3 dB, before proceeding to the experiment. Despite this, what the results suggests is that, at 3 dB, the detection task was still too difficult for the majority of the participants. One way to improve the detectability of the AM probe would be to measure individual thresholds to the AM, and present the probe at threshold level in the experiment. However, the results could also suggest that the AM does not have a strong spatial preference and could appear to the participant that the sound is scattered in other

locations than the side of the adapter. Thus, another way to improve the detectability of the attentional control probe is perhaps to present it in a different modality with a more reliable spatial resolution (such as in the visual modality).

The present results appear to be a combination of several factors such as: the *number of tasks* (two frequencies + an AM detection task + a spatial discrimination task) the *feedback* (which was implemented to build the participant's awareness that he would get more "correct" responses when attending according to the instructions; however, it may have led the participants to search elsewhere to achieve the "correct" feedback) and the *fixed AM level* (the level of the AM was not individualised). The next experiment was design to address some of the major concerns raised in this discussion, with particular attention paid to the attention control probe.

7.3. EXPERIMENT 7 – VISUAL ATTENTION IN ADAPTATION (VAIA)

7.3.1. Introduction of experiment 7 (VAIA)

One of the limitations in the previous experiment 6 was the unreliable attention control feature, which led to inconclusive results. It was not possible to infer about the participants' orienting of attention, which was a vital aspect of the experimental design. This uncertainty was most likely brought upon by the lack of individualised thresholds for the detection of the attentional probe (amplitude modulation), but other factors could have also contributed to lowering the scores of discrimination of the attention probe. For instance, regarding the feedback, it was important to retain a feature in the paradigm that informed the participant that his performance would be better if attending to the instructed side. However, the feedback might have driven the participant to search in a different region from the instructed side, in an attempt to increase the rate of "correct" responses. Furthermore, the amount of events (presented each trial) requiring an action from the participant, whether a covert or an overt one, could have contributed to the confusion regarding the task. These were: attend to high frequency versus low frequency, attend to right vs left, detect if a fluctuation is present in the sound, and finally, judge the lateral location of a target. One aspect missing from the previous experiment was the logging of reaction times (RTs) as this measure could have been used to draw conclusion regarding the difficulty of the task: RTs around 1000 to 2000 ms being expected in tasks with higher cognitive loads or involving stimuli recognition (e.g. Wickelgren 1977) and RTs around 200 to 400 ms are usually reported in cueing tasks of early sensory perception (e.g. Spence and Driver 1998). Furthermore,

RTs can also be useful in controlling for attention orienting, as the use of this measure has long been associated with attention facilitation studies, such as the ones produced by the Posner group. Faster RTs are expected at attended locations when compared to unattended locations.

The main aim of experiment 7 was to investigate if attention orienting modulates the spatial repulsion observable in an adaptation task (same as experiment 6) and to address the methodological concerns of the previous experiment. For this, an attention probe on a different modality was implemented to improve its spatial accuracy: a filled visual circle flashed in either hemifield will replace the AM probe. This change will also allow the removal of the high and low frequency adapter (since the flash can be displayed in the opposite hemifield without the need of a carrier), which will greatly simplify the task. Furthermore, individual thresholds to the attention probe were measured prior to the main experiment and recalled in the main experiment for each participant. Two attention states (attended and unattended) and three adapter conditions (position on the right, left, or absent) were used to test the aforementioned hypothesis: will visually attending to one side of space modulate the size of the auditory repulsion resultant from the auditory adaptation?

7.3.2. **Methods of experiment 7 (VAIA)**

7.3.2.1. Materials

This experiment used the same materials as the previous experiment.

7.3.2.2. Stimuli

This experiment used identical auditory adapters as in section 7.2.2 of the present chapter, with the difference being in the frequency and duration of the sound. In summary, a 1.2 second long adapter comprised by 5 ms noise bursts randomly drawn from two normal distribution of mean ±15° and SD ±10° (positive to the right and negative to the left). The auditory adapters and targets were BBN band passed between 200 and 1200 Hz with a 6^{th} order Butterworth filter. The auditory target lasted 100 ms. Ramp functions were described above in section 7.2.2. The fixation dot used throughout this thesis was lowered in intensity from 2.80 cd/m^2 to 0.19 cd/m^2 and the attention instruction circle (which indicated the side the participant should direct attention) was presented at 0.22 cd/m^2.

7.3.2.3. Procedure

After completing the audiological assessment, the participant was accompanied to a sound treated room where the experiment was explained. A fixation dot (0.2° in diameter) was displayed for the remaining of the trial until the display of a question text. Five-hundred ms (500 ms) after the appearance of the fixation dot, a circle appeared at the left or at the right for 500 ms, indicating the participant which side of the screen he should covertly direct attention to, while maintaining fixation in the centre of the screen. After the attention instruction circle a gap of 500 ms (displaying the fixation dot only) preceded the presentation of one of three adapter conditions: adapter on the left,

right, or no adapter. A filled (grey) visual probe with 1° of diameter, appeared for 16 ms either on the left or right (10° in space) at the same elevation as the sounds (6.4°), with a probability of 0.4 in the attended side and 0.15 in the unattended side. The luminance of this probe was determined before the start of the experiment in the 4 down 1 up adaptive method, described below. During the 1.2 second auditory adapter, the visual probe appeared randomly in a window ranging from 150 ms from the start of the adapter to 300 ms before the end of the adapter. The participant was instructed to press the middle button as fast as possible upon detection of the visual probe. After this sequence of events, a 100ms auditory target was presented in one of seven randomly chosen positions (defined in the previous experiment), immediately followed by "Left or Right?" instructions on the screen. Participants were instructed to press the left or right button on the response box, accordingly. Participants completed 15 trials per target azimuth in all conditions (15 trials ×7 targets ×2 attention conditions [L/R] ×3 adapter conditions [L/R and absent]). To start each new trial, the participant was required to press the middle button. Figure 7-8 illustrates the protocol described here. The visual probe used to control for attention deployment was presented at threshold level, estimated individually prior to the main experiment using a transformed up-down adaptive method, based on Wetherill and Levitt (1965). The visual threshold was estimated with a staircase procedure running three simultaneous, randomly interleaved, adaptive tracks. The procedure required four (4) hits to reduce the stimulus intensity, but only one miss was needed for the reverse (4 down 1 up).

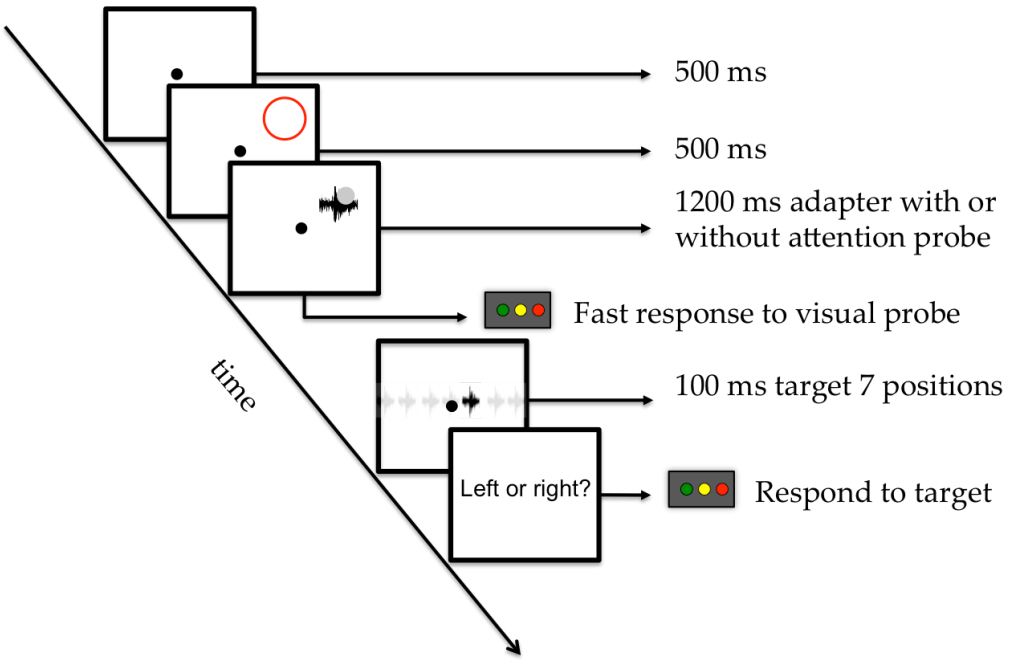

Figure 7-8 Events contained in one trial of experiment 7, that investigates the effect of visual attention in auditory adaptation.

Figure 7-9 shows a screen capture of the Matlab's command window illustrating the simultaneous output (screened in the secondary monitor in the adjacent control room) of the first runs of each track. Here, it can also be seen how the three tracks ran randomly and presented stimuli in different intensities.

```
Track 2: Hit
Track 2: Hit
Track 3: Hit
Track 2: Hit
Track 1: Hit
Track 3: Hit
Track 3: Hit
Track 3: 4 hits in a row - decreasing brightness
Track 2: 4 hits in a row - decreasing brightness
Track 1: Hit
Track 2: Hit
Track 3: Hit
Track 1: Hit
Track 3: Hit
Track 3: Hit
Track 3: 4 hits in a row - decreasing brightness
Track 1: 4 hits in a row - decreasing brightness
Track 2: Hit
Track 3: Hit
Track 1: Hit
Track 3: Hit
Track 3: Hit
Track 1: Hit
Track 1: Hit
Track 1: 4 hits in a row - decreasing brightness
Track 3: 4 hits in a row - decreasing brightness
```

Figure 7-9 Visual threshold estimation using a 4 down 1 up transformed adaptive method.

For example, for this participant, track 3 and 2 were the first to decrease intensity (after 4 correct hits) while track 1 remained in the initial brightness for longer. The initial value of brightness was 255 and intensity was reduced with a step size of 40 in the initial runs (these are virtual numbers not luminance values) until it registered the first miss. After this, the step size would change to 20, 10, and finally 5, with consequent misses. The visual probe was a filled white circle displayed at the same left and right locations as in the previous experiments (details in the General methods chapter). The participant initiated the adaptive method by pressing the middle button on the response box. The participant was instructed to use the same middle button every time he would perceive a flash and to keep his gaze at the centre of the screen, represented by a white dot. It took a minimum of 500 ms and a maximum of 2 seconds after every button press or "miss" by omission for a trial to begin (this as randomised each trial). Figure 7-10 plots two representative participants with distinct evolutions of the adaptive tracks. In order to estimate the threshold, the last 8 reversals of each track were averaged. A reversal was defined as the point in the adaptive track that changes direction. A response was coded as a "miss" after 1 second of inactivity. Thresholds were measured with Gossen Mavo-Spot 2 high precision luminance meter and the luminance values can be found in appendix 6.5.4, table 1. These threshold values were recalled in the attention control condition of the main experiment, when screening the attention probe.

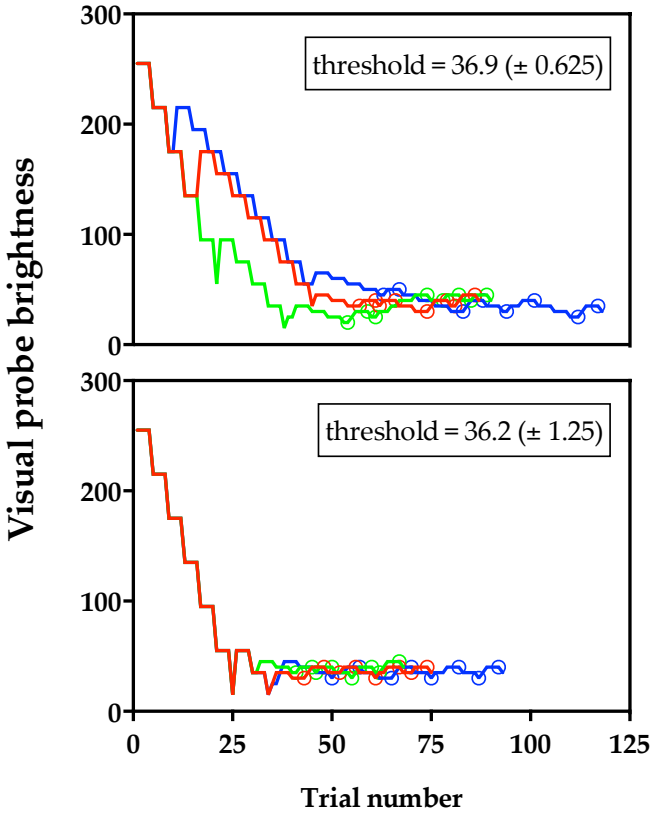

Figure 7-10 Visual threshold plot of two participants. The three colours represent the different adaptive tracks: – track 1. – track 2. – track 3. O last 8 reversals of track 1. O last 8 reversals of track2. O last 8 reversals of track 3. Threshold values are in virtual numbers in the computer code, with SD in brackets.

7.3.2.4. Participants

Fifteen (15) paid participants (7 males) with age ranging from 23 years to 35 (mean age of 27.412 years, SD = 3.893) gave consent to participate in this experiment. Participants had normal hearing as confirmed by a five-frequency pure-tone audiometry (PTA) and were unaware of the purpose of the study.

7.3.3. **Results of experiment 7 (VAIA)**

The percentages of "right" responses were calculated for the seven target locations in the 3 adapter conditions (left, right and absent) and the two attention conditions (attended and unattended). Figure 7-11 shows the averages of the responses to the overall six conditions plotted against the locations of the auditory targets.

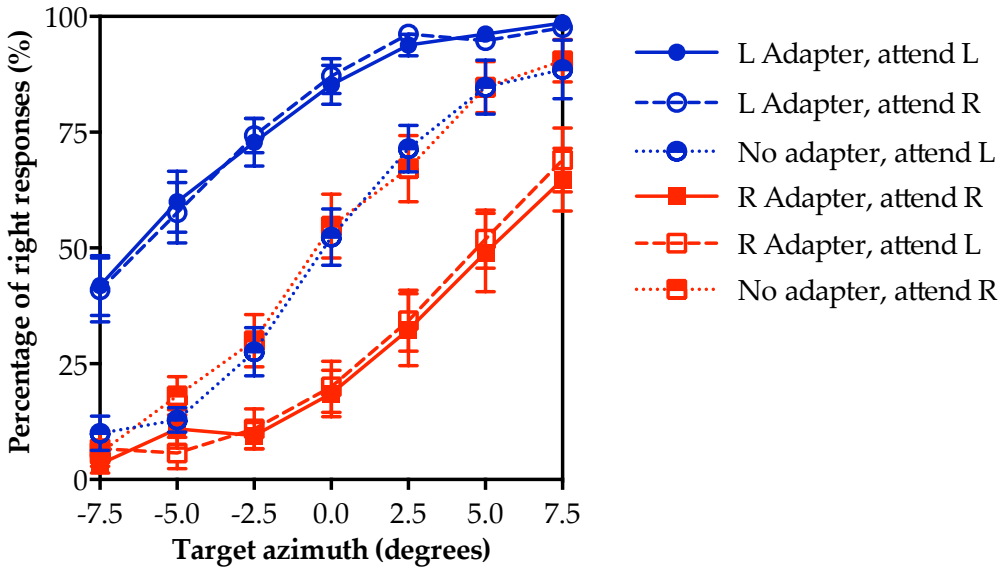

Figure 7-11 Averaged data of experiment 7 containing all tested conditions (n = 14). Error bars are SE.

Solid lines represent the conditions where the location of the adapter coincided with the attention direction. For instance, solid blue lines indicate that the participant was attending right and that an adapter was presented at the same location. The same is true for solid right lines: a right adapter while attending right. Dashed lines represent the inverse: when an adapter was presented in the opposite hemifield to the attention direction. For example, a dashed red line represents an adapter presented at the right, while attention was directed to the left. The dotted lines represent trials with no adapter. Blue dotted lines represent no adapter and attention directed to the left, while red dotted lines represent no adapter and attention directed to the right. The PSEs

were extracted as stated in the General methods chapter. Two participants were excluded for meeting one or more exclusion criteria defined earlier (data for these participants can be reviewed in the appendix C.7.1). Figure 7-12 illustrates the fitting of the NLRM to a representative participant. This participant shows a clear repulsion of auditory targets after presentation of and auditory adapter, in line with the effect observed by Dahmen and colleagues (2010).

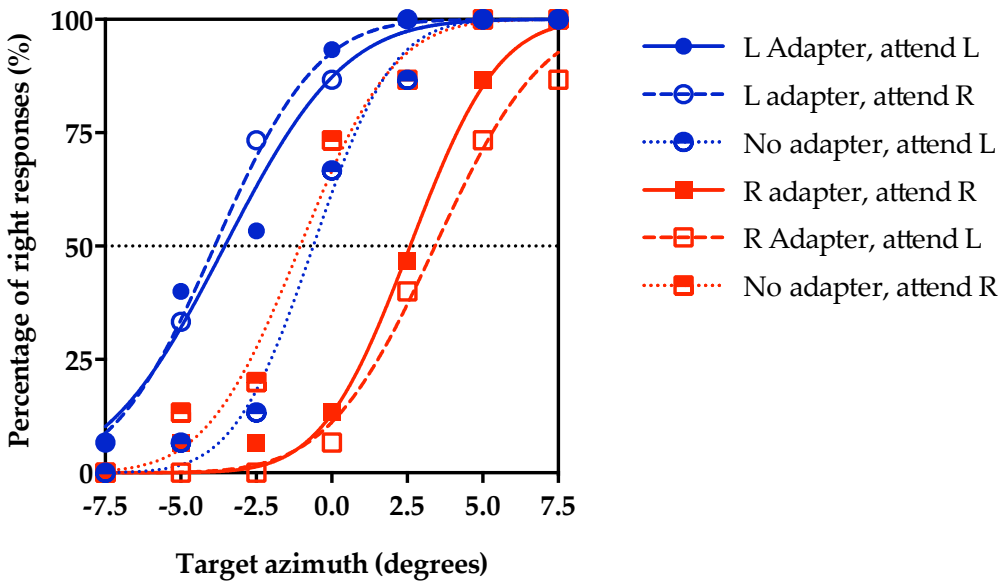

Figure 7-12 Representative participant of experiment 7. A repulsion is evident, represented by blue lines at the left and red lines at the right.

When adapters were presented at the right, the participant responded "left" more often than "right". This can be observed in the red solid and dashed lines that appear shifted to the right at the PSE (the 50% value for the ordinates, here represented by a horizontal black dotted line) and also in the blue (solid and dashed) lines that appear shifted to the left. From this figure (6-14) the direction of crossmodal attention does not appear to influence the spatial perception of the target, since the solid and dashed lines cross the 50% value of the ordinates at close locations and because in the "no adapter" condition, attending to the left or right appears to yield the same PSE (represented by the middle

dotted blue and red lines). This will be confirmed in the following paragraphs.

A 2x2 ANOVA with attention condition (2 levels: attended and unattended) and adapter side (3 levels: right, left or absent) was used to test the how attention modulates the effects of auditory adaptation on auditory spatial perception. No further corrections were applied, as the Mauchly's test of sphericity did not reach significance. The main effect attention was reported as not significant, $F(1, 12) = 1.001$, $p = 0.337$, which indicated that the spatial perception was not modulated by attention deployments. However, there was a main effect of adapter side, $F(2, 24) = 51.265$, $p = 0.000$, indicating that the perceptual bias was influenced by the location of the adapter. Since there was not a main effect of attention, the "attended" and "non-attended" conditions were averaged.

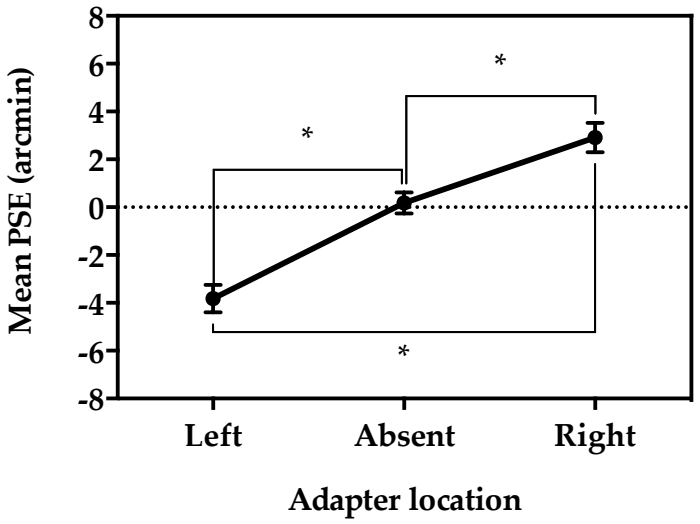

Figure 7-13 Mean PSEs for the left, right and no adapter condition. Asterisks represent significant differences. Alpha adjusted at $\alpha = 0.016$. Error bars are SE.

Post-hoc paired-samples comparisons revealed a significant difference between the "left adapter" (M = -3.820; SE = 0.573) and the "right adapter" (M = 2.916; SE = 0.615), T (12) = -7.65, p = 0.000; between the

"no adapter" (M = 0.181; SE = 0.437) and left adapter conditions, T(12) = -6.043, p = 0.000; and between the "no adapter" and right adapter, T(12) = 7.596, p = 0.000. The alpha threshold for the above paired samples statistic was adjusted using the Bonferroni method for multiple comparisons (α = 0.016). Figure 7-13 illustrates these results. A further one-sample T-test reported that the bias at the "absent adapter" condition was not significantly different from zero, thus an outcome measure of bias was computed, in line with previous chapter. The left bias was defined as the PSE of the left adapter minus the PSE of the "no adapter" condition; and the right bias was defined as the PSE of the "no adapter" condition minus the PSE of the right adapter condition. A one-sample t-test was used to investigate the significance of the repulsion. Both left (M = -4; SD = 2.38; T[12] = -6.043, p = 0.000; ES = -3.49) and right biases (M = -2.7; SD = 1.29; T[12] = -7.596, p = 0.000; ES = -4.39) were reported as significant repulsions, as shown in figure 7-14.

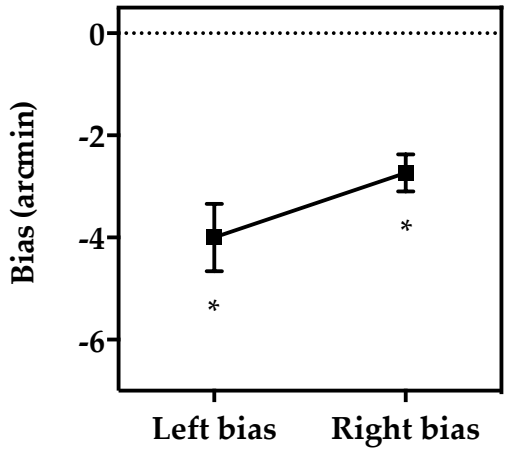

Figure 7-14 Perceptual bias across each adapter location. Asterisks denote a significant departure from zero. Error bars are SE.

In order to determine if the visual probe was successful in controlling for attention deployment, measures of reaction time (RTs) and d prime (d') were calculated. The d' measure informs about the ability of the participant to discriminate the appearance of the attention probe. Since

the probe was also presented at unattended locations (with less probability) it was expected that the d' would be significantly lower than at attended locations. This meant that the participant was able to discriminate better the appearance of the probe in the same location where attention was being directed. To support the results from the d' measure, reaction times were calculated. The participant was encouraged to answer as fast as possible to the appearance of the probe, regardless of its location. It is expected that RTs at attended locations are faster than at unattended locations, according to the well-studied "Posnerian" attention facilitation literature. A paired-sample t-test was used to compare attended an unattended conditions. Both measures of d' and RTs report significant differences at the attended locations, as depicted in figure 7-15.

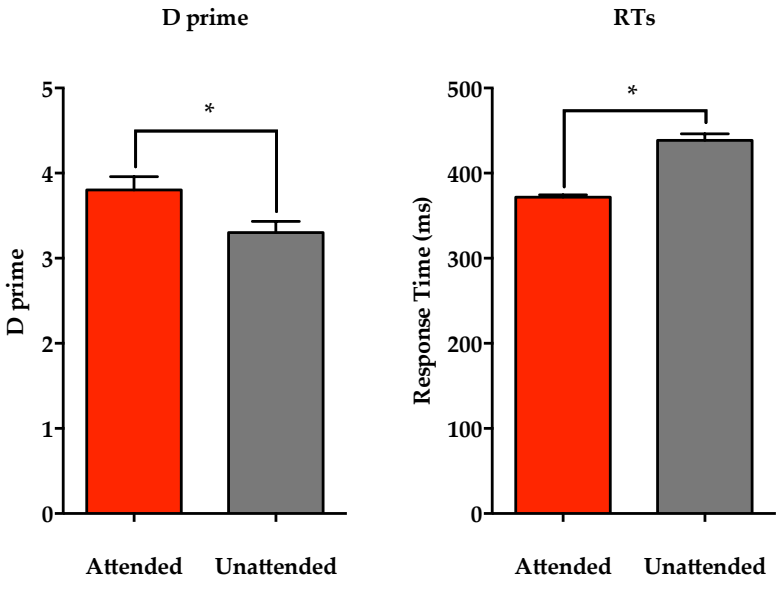

Figure 7-15 D prime and reaction time measures of the responses between attended and unattended conditions. Error bars are SE.

Participants were able to have better discrimination (T[12] = 5.94, p = 0.000) and also presented faster reaction times to the probe (T[109] = 7.56, p = 0.000) at attended locations than at unattended locations.

7.4. INTERIM DISCUSSION OF CHAPTER 7

In this chapter I addressed the question whether attention could modulate sensory adaptation. Historically, attention and adaptation are studied in isolation, but, as stated in the literature review of this thesis, often studies of spatial attention use paradigms that can induce states of sensory adaptation, since the same stimuli is presented thousand of times, needed to compute response the averages (as, for example, in the case of the behavioural experiments conducted in the present thesis). This chapter included two experiments. The first experiment (experiment six), investigated the role of auditory attention in an auditory adapter. The adapter stimulus used was an adaptation of Dahmen et al (2010), which was found to induce a spatial repulsion of the target away from the side of the adapter. The d' values indicated how well the participants discriminated the attention control probe (an amplitude-modulated signal embedded in the adapter), but, when comparing d's at attended locations and at unattended locations, there were no significant differences, which indicated that the attention control probe was of poor reliability. Thus, no inferences could be drawn regarding the influences of attention on the adaptation. Nevertheless, the results replicated Dahmen et al findings: a clear repulsion of the targets away from the side where the adapter was resented. A follow-up experiment (experiment seven) aimed at addressing the limitations found in the methodology of experiment six, such as the inaccurate control for attention allocation, revealed that attention deployments did not contribute to the spatial repulsion. The findings of this chapter will be discussed in greater detail in the general discussion of this thesis.

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CHAPTER 8 GENERAL DISCUSSION AND CONCLUSIONS

Despite the overwhelming quantity of studies in attention, little consideration has been given to the benefits or the costs of attentional deployments when the region of interest (the foveated location) is different from where the exogenous event occurred. A sudden exogenous deployment of attention to an unimportant location might neglect the main location, causing a perceptual bias. This has been shown in the past by Suzuki and Cavanagh (1997) who found errors in reporting a central target away from the location of peripheral (left or right) exogenous cues. This discussion will start by briefly summarising the general aims of the thesis and specific aims of each experiment. In subsequent sections, the main findings of each chapter and their implications will be discussed in greater depth.

8.1. SUMMARY OF RESEARCH AIMS

The general aim of the present thesis was to explore how extrapersonal space is maintained or altered in the presence of surrounding irrelevant stimuli (either in the same modality or in a different modality) by studying the ARE under visual and auditory modalities (and combinations of both). In doing so I also aimed to test previous notions that the ARE is reliable and of easy reproducibility (Pratt and Arnott 2008). To achieve this, specific research aims were set, arranged into the chapters that comprise this thesis: experiments one and two (chapter 4) aimed at adapting the ARE to test auditory targets. This paradigm flashed a circle at one of three locations (left, middle or right) followed by a sound, which participants were asked to localise, coming from the left or the right (VA ARE). Unlike the unimodal visual ARE of Suzuki

and Cavanagh, the results showed that, much like the ventriloquism effect, the localisation of sound stimuli were judged towards the location of the visual cue. This was termed in this thesis as the attentional attraction effect (AAE), but later sections will discuss how this effect may differ from the AAE reported by Ono and Watanabe (2011). Experiment three (chapter 5) tested the perceptual influence of irrelevant auditory cues on the spatial discrimination of visual objects (AV ARE). This experiment addressed some methodological issues with the previous study by Arnott and Goodale (2006), and extended it by investigating the time-course of the resulted repulsion. Both chapters (4 and 5) addressed two fundamentally different versions of the crossmodal ARE; one, studied auditory performance, while the other studied visual performance. For this reason it is likely that different generators are behind each phenomenon. Experiments four and five (chapter 6) were concerned with studying unimodal versions of the ARE. In experiment four, I aimed to replicate and clarify the time-course of the original ARE reported by Suzuki and Cavanagh. The results from this experiment were two-fold in that it confirmed the repulsion at early ISIs, but did not followed the same trend in later ISIs (repulsion dissipated after 50 ms of ISI). This is believed to be mostly due to methodological differences, which have already been addressed in the interim discussion of chapter 6 (section 6.3). In experiment five I adapted the unimodal visual ARE used in experiment four to study the existence of an exclusive unimodal auditory ARE. This experiment presented the participants with an auditory cue, followed by an auditory target, which participant were asked to lateralise. The results failed to confidently show a bias (either repulsion or attraction) of auditory targets, which led to the conclusion that the ARE is either very hard to demonstrate in the auditory modality, or might not occur at all

in this sensory modality. Lastly, chapter 7, investigates the possible contribution of adaptation in an attentional task, since most psychophysical paradigms (like the ARE) repeat their stimuli thousands of times, often without interruption. Two different experiments were design for this aim; in experiment six, participants were required to selectively attend to an amplitude-modulated sound in order to detect it embedded in an (auditory) adapter. Following this, participants were asked to localise a noise burst. This experiment adapted a paradigm by Dahmen et al (2010) in which an auditory adapter repulsed the location of auditory targets towards the opposite side, however, the results were inconclusive, mainly due to methodological aspects like the poor reliability index of the attentional probe. These have been discussed in the interim discussion of the experiment (section 7.2.3). Experiment seven aimed to address these issues by re-designing the experiment and implementing a number of changes (see introduction of experiment seven, section 7.3.1) The results show that attention did not modulate the adaptation.

The pages that follow will discuss in greater detail the finding of experiments that investigated the ARE in unimodal conditions, in crossmodal conditions, and those concerned with attention in adaptation.

8.2. DISCUSSION OF FINDINGS

8.2.1. **Unimodal ARE (visual and auditory)**

This thesis investigated the attentional repulsion effect (ARE) in its unimodal visual (VV; experiment four) and auditory (AA; experiment five) forms in chapter six (sections 6.1 and 6.2, respectively). In the case of experiment four, not only was the visual (VV) ARE was not observed

for ISIs above 200 ms, but also the observed repulsion (2.5 arcmin) was smaller than the repulsion observed in other studies (9 arcmin, Suzuki and Cavanagh 1997; around 4 arcmin for Kosovicheva et al. 2010; Ono and Watanabe 2011). However, none of the studies of the ARE, so far, report effect sizes (ES). This is peculiar since it is very easy to calculate the ES and it is a useful tool to understand the significance of the finding. In our experiments our effect sizes were large (d = 1.34, 50 ms ISI; d = 1.04, 100 ms ISI), and since ES is a way of quantifying the difference between the bias and the hypothetical zero bias (not confounded by the sample size) the results show a robust ARE. However, the effect observed in this thesis might have been reduced in amplitude by the methodology. Comparing the methodology used in the present thesis with the original 1997 study (Suzuki and Cavanagh 1997), the differences are evident, even from a macro perspective. While I used the method of constant stimuli (MCS) to measure the repulsion amplitudes, Suzuki and Cavanagh used and adaptive staircase method. Adaptive methods are generally considered better as they present some advantages over the MCS: adaptive methods do not require the researcher to have a prior assumption of where the threshold region is located in the stimuli set (which is what happened for several participants in the unimodal auditory ARE experiment); furthermore, adaptive procedures are generally more efficient as they require less trials to reach a threshold (Watson and Fitzhugh 1990). However, it would be surprising if this significantly changed our findings, since several studies were already successful in reporting an ARE using the MCS (see for example Pratt and Turk-Browne 2003; Arnott and Goodale 2006; Chow et al. 2014). But, of particular importance in the MCS used in the present thesis (that contrasts somewhat with the MCS used in the ARE literature) might have been the amount of uninterrupted trials

required to complete the experiment, which could have fatigued the participant. All of the referenced studies planned a session break within the first 100 trials, while the participants in our experiments completed the 300 trials without breaks. Nevertheless, it is more likely that the sum of all the small discrepancies from our experiment played a bigger role in reducing the ARE's amplitude. These were mentioned in the respective section (*6.3.2*), but are restated here for convenience: the use of a dual cue paradigm in the literature, which would have repulsed both the top and bottom line of the vernier, thus causing a bigger repulsion effect (I used a single cue paradigm); the shorter seating distance in our experiment (45 cm) was a culmination of several factors such as the size of the room and the distance of the response box to the patchbay located in the wall, but ultimately, since several studies had used similar distances in the past, I opted for a compromise between experimental set-up and successful distances from the literature (44 cm Pratt and Turk-Browne 2003; 44 cm DiGiacomo and Pratt 2012; 44 cm, Gozli and Pratt 2012; 48 cm Chow et al. 2014). However, this could have decreased the spatial resolution of the vernier offset displayed on the screen. Lastly, the masking squares of the Suzuki and Cavanagh study were four times brighter than ours, which would have better disrupted the vernier afterimages, contributing to a stronger ARE. However, one aspect in particular is believed to have a greater contribution: the difference in methods for calculating the bias. The ARE observed in this thesis is calculated by taking an average of two cue positions using a central measure of bias, which is measured with the same amount of trials as the left and right bias. In contrast, Suzuki and Cavanagh and Arnott and Goodale took the bias value given by a single cue location. As explained before, if the left, middle and right cues have biases of -7

arcmin, -6 arcmin and -5 arcmin, respectively, the measured ARE would be:

$$\frac{([-7]-[-6])+([-6]-[-5])}{2} = -1\ arcmin$$

in this thesis, and would be -7 arcmin in Suzuki and Cavanagh and in Arnott and Goodale's study. It is evident that this creates a considerate disparity between ARE amplitudes, thus the need establish measures to quantify the ARE.

Regarding the unimodal auditory ARE, we have seen (in the literature review of this thesis) how the visual system is better equipped to code space, in comparison to the auditory system. In this thesis I attempted to investigate if the ARE, that is traditionally studied in the visual sciences, is truly modality (visual) specific, or if other modalities can generate such effect. If one considers that the ARE is brought upon by shifts of attention, and in turn, if one considers that attention might be a supramodal phenomenon (Spence et al. 2000; Lakatos et al. 2009; Green et al. 2011), it should not matter in which modality the distractor (that draws attention) is presented to the participant. This is perhaps the reason why the ARE can successfully be evoked using visual or auditory cues, as long as the target modality remains visual.

In this thesis we attempted to show a purely auditory ARE, but the results are inconclusive. This is mainly due to errors in picking the stimulus levels, leading to 21 participants being excluded from the data analysis. As a result, the question of whether the auditory modality is capable of producing an ARE was not satisfactorily answered and is still an open topic.

The literature reviewed in section 2.2.3 suggests that the auditory system is not as accurate as the visual system in determining the

location of objects. In fact, in support of this notion, the minimum audible angle of humans[36], measured in both the horizontal and vertical plane, is around 1° and 3.7°, respectively (Perrott and Saberi 1990; but see Moore 2004). Considering that the spatial errors in the visual modality measured in the first experiment were around 2 arcmin (0.03 degrees of arc) and were reported to be around 0.1° in other studies (Suzuki and Cavanagh 1997; Kosovicheva et al. 2010; Ono and Watanabe 2011), this is indicative of the superior spatial resolution of the visual system. Thus, it is possible that the auditory system might not be capable of the same precise spatial judgements, having a much grosser resolution. This would predict that the auditory ARE is perhaps impossible to measure with behavioural methods or even maybe impossible to be generated by the auditory centres in the brain.

In summary, when we consider the unimodal auditory ARE, it is possible that the auditory system might not be able to generate such effect. This can be linked to the fact that the auditory system has difficulties in resolving spatial locations within 1º in horizontal space (Moore 2004), which is precisely where the ARE operates (0.16 degrees in Suzuki and Cavanagh 1997). Recalling the spatial coding section of the literature review (section 2.2), the visual system is able to directly code positions in space by neurons in the retina while the auditory system relies on further computations between the ears to infer a spatial locations.

8.2.2. **Crossmodal (audio-visual or visual-auditory) ARE**

The ARE was investigated in two crossmodal conditions in this thesis: the first tested auditory influences in visual perception, while the other

[36] Or in other words, the just noticeable difference in angular displacement that a listener can perceive.

tested visual influences in auditory perception. For this reason this section will comprise two sections, the AV ARE paradigm and the VA ARE paradigm.

8.2.2.1. The AV crossmodal paradigm

In 2006, Stephen Arnott and Melvyn Goodale published a study in which they replicated the original ARE and further demonstrated that replacing the visual cues with a sound also yields an ARE. To date this is the only study of the ARE that uses two different modalities to generate the effect: an auditory cue that exogenously grabs attention, and a visual target to measure the perceived bias. In chapter 5, I revisited this paradigm and addressed a number of questions. In their study, Arnott and Goodale tested two ISIs, 50 and 100 ms, but reported a significant repulsion only at 100 ms. This suggests that the AV ARE takes around 50 ms to develop, but since the authors did not investigate further temporal asynchronies, it is unknown whether the effect continues to increase, plateaus, or decreases, after 100 ms. One of the aims of that chapter was to address this issue by studying the temporal dependency of the AV ARE. I successfully extended Arnott and Goodale 2006 study and observed a repulsion effect as early as 16 ms of cue-target interval that was consistent throughout the entire ISI range (16-500 ms).

One issue left to discuss in this section was the fact that at ISI 500 ms, the bias induced by the right cue was significantly (and surprisingly) smaller from the bias introduced by the left cue. This is an unusual result given that the size and polarity of the left bias did not differ from the right bias for all the previous ISIs. Furthermore, the remaining experiments also confirmed that spatial bias does not differ across hemifields. At this cue-target latency (500 ms), the effects of exogenous

attention would have faded away (Eriksen and Collins 1969b; Eriksen and Rohrbaugh 1970b; Suzuki and Cavanagh 1997), however, attentional influences could still be possible through endogenous mechanisms (Posner 1980). This is unlikely as the participants were given instructions to focus on the target modality (visual), thus attention was likely to be covertly directed to the small region in space where the targets appear. After 200 ms have passed from the presentation of the auditory cue, attention was likely to have drifted away from the cue position (Nakayama and Mackeben 1989; Suzuki and Cavanagh 1997), and returned to the fixation dot and the region of space surrounding it (where the vernier targets were presented). However, we cannot be certain of this. One possible explanation is that the location of the cue was retained in memory, but studies indicate that when memory is involved, the resulted bias is of inverse polarity (AAE, attentional attraction effect; Ono and Watanabe 2011; Yamada et al. 2011). In future studies, a masker could be introduced to disrupt the memory of the cue, however, care needs to be taken when designing the experiment in order to disambiguate between cue-induced bias or masker-induced bias. Thus far I am not aware of any studies indicating that cueing produces different bias (in terms of magnitude and/or polarity) depending on the stimulated hemifield. My interpretation is that this result is heavily depend on how the statistical tests are read, especially since the result was significant at alpha = 0.04, and has a small effect size (r = 0.36). As Frick (1995) points out, appropriate criteria should be taken in consideration when accepting the null hypothesis: 1, H_0 must be possible; 2, results must be consistent with the H_0; and 3, enough has to be done to assure that the experiments were

designed to test the H_0. All of the above criteria were met in our experiment. The present null hypothesis is possible[37], which was confirmed by the results at all other ISIs in the present experiment three. Furthermore, these results were also confirmed in the other ARE experiments of chapter four and six, indicating that the trend is that there is no differences between the biases created by the left or right cues. The fact that the null hypothesis is plausible is also supported by Arnott and Goodale's (2006) results, which is the only study to date to investigate the crossmodal ARE under identical conditions of cue and target stimuli. More importantly, the effect size of this test was very small. Cohen (1990) stresses the importance of effect sizes over statistical alpha thresholds, and explains that studies should be designed to ensure that there is at least 80% probability of detecting an effect where there is one to be detected (Cohen 1990, 1994).

8.2.2.2. The VA crossmodal paradigm

Chapter four investigated a novel experimental paradigm constructed from the classical ARE that tested the attentional effects of a visual cue on auditory target localization. The following discussion will speculate on the different mechanisms that can be operating before and after 100 ms of cue-target interval. In the experiments of chapter four, participants were asked to judge the location of a sound and to ignore the preceding visual stimulus appearing randomly in the middle, left, or right. The result shows an attraction of the auditory targets towards the side of the visual cue. It is not unreasonable to associate visual dominance to spatial percepts and auditory dominance to temporal percepts (Recanzone 2009; Stein 2012) and in fact, both experiments in that chapter show that the spatial percept of a sound is attracted to the

[37] H_0 = there is no difference between left and right bias

position of a flash. But, what could be the mechanisms underlying these results? The following discussion is divided into several sections, each one considering the possible neural contributors to our VA ARE results.

Ventriloquism illusion

Often attraction effects are attributed to the ventriloquism illusion but, with the introduction of a cue-target asynchrony, this illusion may not be the major contributor to the observed effect. Nevertheless, at shorter ISIs (16 and 50 ms) the ventriloquism illusion needs to be considered. The ventriloquism illusion is an attraction of auditory targets towards the side of a synchronously presented visual stimulus. However, going back to the notion of stimulus synchrony in the ventriloquism illusion, simultaneously presented stimuli may not be physiologically synchronous. Due to the particular transducing method of each sensory system, it takes longer to perceive the onset of visual events than it takes to perceive the onset of auditory events (simple detection of auditory targets is 25-50 ms shorter than visual targets; Dinnerstein and Zlotogura 1968; Elliott 1968). Thus, if a sound is presented 25-50 ms after a flash, these events may still be perceived as presented in synchrony. Furthermore, Thorne and Debener (2008) measured perception of visual-auditory stimulus simultaneity and reported that within -10 ms to 80 ms[38], this perception was maintained. Since in present experiment the 16 ms ISI and the 50 ms ISI are within this range, it is reasonable to believe that, during these two ISIs, the visual and auditory events will have been perceived in synchrony. I can therefore conclude that, at very short ISIs (16 and 50 ms), the auditory target was attracted by the visual distractor, in line with the ventriloquism theory. This means, on the other hand, that if we are

[38] -10 ms indicating that sound came first.

looking for attentional influences using a visual cue and auditory target, these can only be measured from 50ms onwards because several studies indicate that the ventriloquism illusion is immune to manipulations of attention. Bertelson and colleagues (2000) and later Vroomen, Bertelson and de Gelder (2001) in a series of studies showed that the ventriloquism illusion represented an automatic mechanism of sensory interaction and was not related to either endogenous or exogenous attention. Further evidence dissociating the ventriloquism effect from attention is given by Stekelenburg, Vroomen and de Gelder (2004), as the authors showed that the ventriloquism effect evoked an auditory Mismatch Negativity (MMN). MMN has long been found to be independent of attention manipulations by Näätänen and colleagues during the late 70s, mid 80s (but see Näätänen et al. 2007 for a review of the topic).

The AAE (attentional attraction effect):

Ono and Watanabe (2011) reported for the first time an attentional attraction effect, albeit in unimodal conditions of visual stimulation, not crossmodal. The authors flashed two sudden circles in an opposite diagonal, randomly followed or preceded by a vernier display. The participants were asked to judge if the top line of the vernier display was to the left or to the right of the bottom line. The top line was perceived to be shifted away (*repulsion*) from the cue location if the cue was presented before the target. Conversely, if the cue was presented after the target, the top line was perceived to be shifted towards the cue location (*attraction*). The authors also varied the cue-target asynchrony and, in line with experiment one of this thesis and the aforementioned reports of exogenous attention, the attraction and repulsion peaked, in both cases of cue first and cue second, at ISIs of 100 and 200 ms.

Attentional shifts were confirmed by replicating the results using an endogenous attention deployment paradigm. In the case of the attraction effect, Ono and Watanabe (2011) argued that attention retrospectively influence the perception of the target. Moreover, the temporal range that the effect seems to operate is well inside exogenous deployment of attention. However, our results indicate an attraction that is present without retrospective influences. It is possible that the AAE measured in this thesis is not the AAE observed by Ono and Watanabe. In fact, the AAE measured here might not be due to attentional mechanisms. If the effects of exogenous attention fade away after 200 ms (Eriksen and Collins 1969a; Eriksen and Rohrbaugh 1970b; Colegate et al. 1973; Nakayama and Mackeben 1989), then it is unlikely that exogenous attention is present at 1000 ms. Attentional influences could still be involved through endogenous deployment (Funes et al. 2005; Chakravarthi and Vanrullen 2011) however, because the instructions were to ignore the cue and judge auditory targets, it is unlikely that 1000 ms after the cue the participants would still be sustaining their attention at the cue location. Since targets and cues never existed at the same spatial location, it is plausible that after the 200 ms ISI the participants' attention would have scattered over the entire frontal space, searching for the sound. Thus, at 1000 ms ISI, attention (exogenous our endogenous) is not likely to be involved. Considering the above, it is possible that the AAE measured in this thesis is not ARE related.

One field of science that investigates visual sensory memory helps disambiguate this result. Visual stimuli are known to remain visible after the stimulation has ceased, a phenomenon named visual persistence (Coltheart 1980) or phenomenal persistence (Turvey 1978).

This can be experienced when, in a dark room, a flashlight is waived in a circular motion and, despite the light being a discrete point in time, a continuous circle is seen, if the flashlight moves fast enough. Moreover, information about the stimulus is available to the viewer in the persisted image and can be retrieved for a short period of time after the stimulus offset (Sperling 1960) sometimes for as long as 1 second (Averbach and Coriell 1961). Thus, it is possible that the location of the cue was retained in short-term memory. Sperling proposed that visual information is stored in a rapidly declining system (later called the visual sensory memory). Another form of lingering visual phenomena that could have contributed to the attraction reported in this thesis are non-foveal afterimages. Afterimages are fundamentally different from persistence in that they are the negative polarity as the original image, they require an intense flash, are longer in duration and are not as easily masked as persistence images (Irwin and Thomas 2008). The resultant afterimages from the cues were not controlled properly in the experiments of chapter four and, a negative afterimage of the circle could have been present during the presentation of the auditory target. This could have automatically biased the auditory perception towards the location of the visual afterimage.

Nevertheless, one cannot discard response bias from these results, nor erroneous responses (responding right when intended to respond left). Eve though these might influence the results, the experiment was design to limit these effects. To have a meaningful impact in the results, the participant would have to be very consistent in their "errors" for them to be meaningful across the 315 trials comprised in a single condition. If this was the case, then the errors could actually represent the participant's sensitivity to the stimuli, and in this case, the "error"

becomes the participant's actual performance. Since this was a paid experiment I believe the participants' results do reflect the true perceptual sensitivity and that the effect of any response errors that might have occurred (which I also believe to be true) would be minimised in the averaging process.

Other contributors:

In the VA ARE, spatially uninformative cues appeared at one of three positions each trial (-10°, 0° and 10°) in a random order. For this reason, the participant could not have anticipated the location of the cue, thus being unlikely that voluntary covert orienting of attention could have contributed to the effect. This leaves exogenous attentional deployment as one of the possible candidates. Also, targets and cues were displayed in different horizontal and vertical positions (cue-target position difference ranging from 2.5° being the closest to 17.5° being the widest separation), therefore the presence of a priming effect would be unlikely. Furthermore, even though inhibition of return (IOR) is a supramodal phenomenon present in all cue-target combinations of visual auditory and tactile modalities (Spence et al. 2000), both cue and target need to be presented at the same spatial location (Spence and Driver 1998; Chica et al. 2006; Lupianez et al. 2006; Tian and Yao 2008; amongst others) for IOR to be observed. Our paradigm presented spatially distanced stimuli, thus bypassing IOR phenomena.

It is reasonable to speculate that the neural substrates of the visual attraction effect shown in experiments 2 and 3 could be related to gating between sensory cortices. Johnson and Zatorre (2005) showed, using fMRI, that when attending to one modality, there is a gate on the activity of the ignored modality. This interaction can potentially enhance the attended modality at the expense of the gated modality; in

our paradigm we have shown that the unattended modality incurs localisation errors that can be due to automatic orienting of attention to the other modality. It is possible that by gating the auditory modality, the brain will need to rely more on spatial cues given by the visual modality to make perceptual judgments. Thus, the fusion of the two events will have bigger contributions from the visual modality, which could help explain why sounds were perceived towards the flashes.

8.2.3. **Attention in adaptation:**

In the literature review I argued that sensory adaptation could be a contributor to the ARE (particular in faster paradigms with short ISIs), since the psychophysical stimuli are presented consistently and uninterruptedly during 20-minute sessions (in our case). However, few studies have investigated attentional influences in sensory adaptation, especially in a paradigm like the ARE. This was the aim of chapter seven. This chapter presented two (complementary) experiments to study the combined effects of attention and perceptual adaptation.

The results from the first experiment were inconclusive regarding the attentional influences (due to the attention probe being unreliable) but regardless of the attentional hypothesis, the results showed that the observed repulsion (by the adapter) is independent of pitch. A spatial bias was observed under both low and high frequencies of adapter--target combinations and the size of this bias was shown to be identical. This is intriguing because it suggests that a low frequency adapter can promote adaptation of high frequency targets. Low frequency adapters would be expected to fatigue low frequency cells, not high frequency ones. As we have seen in the literature review (chapter 2; specifically, section 2.2..2), the auditory system is tonotopically organised and neurons that code low frequency sounds are localised in the apex of the

cochlea while high frequency neurons are placed at the other extremity, the base. Thus, to contemplate that adaptation of neurons that code high frequency sounds by using low frequency adapters, one has either to consider an extremely plastic brain or a fusion of these inputs at a higher perception level. In support of this, receptive fields of neurons were thought to remain fixed in their position and shape, but this notion was questioned first in the auditory community by Weinberger and colleagues, almost twenty year ago (Weinberger 1998, 2003, 2013; Fritz et al. 2007b) and later in the visual community (Duhamel et al. 1992). Fritz and colleagues (Fritz et al. 2003, 2005a, 2005b) showed that receptive fields in A1 are dynamically reshaped (shifted) by task conditions and attentional focus. Furthermore, evidence of a nimble, plastic and adaptive brain can be found in the spike-timing-dependant-plasticity (STDP) phenomenon, where plastic changes depend on spike order and timing of the pre and post-synaptic activity[39]. Dahmen and colleagues (2008) were able to show that the preferred frequency (PF) of a neuron can be shifted via repetitive pairing with non-preferred frequency (NPF). Positive conditioning (NPF stimuli first and PF stimuli second) shifted the PF of the neuron towards the side on the NPF, while negative conditioning (PF stimuli first and by NPF stimuli second) was reported to further tune the neuron's centre frequency towards and around the PF. This has also been shown in crossmodal conditions, where responses of neurons in the superior colliculus that began as two seemingly independent unisensory responses (to visual and to auditory stimuli) tended to "merge" during repeated presentation of a sequential cross-modal stimuli into what appeared to

[39] Otherwise known as the Hebbian rule of associative synaptic plasticity, which has been proposed to be the basis of synaptic learning, through long term potentiation (LTP) and/or long term depression (LTD; Hebb 1949; however see Markram et al. 2011, for a detailed review of this topic).

be a single response (Yu et al. 2009). Under unimodal visual conditions, timing-dependant plasticity has been shown to change the perception and identification of faces (see appendix C.7.2; McMahon and Leopold 2012), and to induce shifts in the orientation tuning of cortical neurons in V1 of anaesthetised adults cats (Yao and Dan 2001). Despite these findings, it should be acknowledge that the dynamic remaps of RFs mentioned above were accomplished when both stimuli share some characteristics. One study in particular was able to show adaptation as a function of adapter-probe frequency separation (Δf; see appendix C.7.3). Adaptation is stronger when there is no Δf, but it is still present (although in a lesser degree; 50% adaptation) when the Δf is as high as 1.5 octaves (Briley and Krumbholz 2013). Likewise, the above-mentioned study by Dahmen et al (2008) supports this notion by showing shifts in the PF when the frequency separation of the conditioning stimuli was as high as one octave. In the present thesis, the Δf was either zero (when the frequency of target and probe matched) or three octaves apart (e.g. low frequency target [500 Hz] and high frequency target [4000 Hz]). Taking this evidence into account, it would seem unlikely that our adapter would produce an identical effect when our Δf was zero than when it was 3 octaves apart. In my view participants struggled to understand and complete this task and as such, the results are very unreliable (also denoted by the results of the attention probe), one of the disadvantages of behavioural studies.

The second experiment designed to address important methodological concerns that were not working in the first experiment, mainly concerning the control of attention allocation. In summary, the results from the second experiment show that the attention probe was successful in controlling for attention deployment with the classical

attention facilitation effects being observed (Posner 1980; Posner and Cohen 1984; Posner and Petersen 1989): participants responded faster (as indicated by RTs) and were able to discriminate more accurately (as indicated by the d' results) when the probe was presented at the attended side. It was postulated that, considering an auditory adapter on the "right", if the participant is attending "right", the repulsion effect would be bigger than if the participant attended to the opposite hemifield. In other words, if attention was directed to an adapter, it would repel the targets to a greater extent than if attention is directed in the opposite side. This was not observed. A repulsion was present as a result of left and right adapters, in accordance with Dahmen et al (2010), however, attention effects were not observed, despite the attention control suggesting a correct attention orienting. Attention was not shown to modulate the adapter effects on the target, in all three adapter conditions: left, right and no adapter. Two explanations for this result are possible. One, it is conceivable that the null hypothesis is in fact true and attention does not influence adaptation. Two, it is possible that the results reflect methodological constraints: the designed paradigm is not sensitive to attentional manipulations. The first explanation is questionable since attention is likely to be present during the behavioural task: "Attention comes in three parts: arousal, orientation and focus. This means you first of all need to be alert enough to attend to something, then you direct your attention to the particular stimulus and finally you focus on it" (Collins 2016, p 107). To construct perceptual judgments, a minimum state of vigilance is assumed; in the present experiment, the presence of an attention probing cue (a flash) would have, according to the seminal studies of reflexive, automatic, or bottom-up attention, drawn attention exogenously towards its location. Thus, attention was likely to be

present in our results, and the size and the direction of the spatial shifts are in accordance with Dahmen et al (2010), suggesting a successful perceptual adaptation. For this reason, the results might, instead, show the difficulty of recording behaviour adaptation effects, separate from attentional ones. The second explanation is consequently more plausible in the present context: the designed paradigm is not sensitive enough to be able to observe attentional effects in a Dahmen-like adaptation task. Here we must consider three important aspects of attention: one, much like a volume knob in an amplifier, attention can be turned up or down, however, being a finite resource, if it is mainly allocated to process stimuli from one task, less resources are available for another simultaneous concurrent task; two, it is possible to divide attention (across space and across stimulus modalities) according to each individual's processing capacity; and three, exogenous attention is contingent on the amount of common features that both cue and target share. To relate these three aspects with the results, we first must revisit the task. Participants were first asked to respond as fast as possible to a visual probe, and only after, judge the location of a target. However, the flashed probe appeared during the presence of an adapter. This predisposed the participant to be in a selective attention state during the bimodal presentation condition, which would involuntarily mandate that the participant's attention would be divided across space (since the probe would appear randomly at one of two locations, left or right) and across modalities (auditory adapter and visual probe). All of these will have used attentional resources. Johnson and Zatorre (2005, 2006) have shown, using fMRI, that actively attending to the auditory modality led to increased activity in the cortices subserving that modality and decreased BOLD (blood-oxygen-level-dependant) response in the cortices subserving the visual modality. The opposite

was also shown. This suggests that attention is a finite resource that needs to use a system of sensory gates to cope with the environmental demands. Thus, in our experiment, (aspect one) increasing attention to the visual modality (aspect two) would have reduced the amount of resources available to the auditory modality, even if both had a certain degree of automaticity in drawing attention (both onsets of probe and adapter would have driven a covert attention orienting). Importantly, this automatic attention orienting brings us to the third aspect: reflexive covert orienting has been shown to be contingent on the behavioural goals of the observer (also known as attention control settings or ACS). Attention orienting by irrelevant peripheral cues will draw attention depending on the amount of critical features that they share with the target (Folk et al. 1992). Furthermore, several studies have shown that ACS can "effectively override the stimulus-driven capture of attention" (p.296, Adamo et al. 2008), even in the case of very salient cues that do not share critical features with the searched target (Remington et al. 2001; Folk et al. 2002; Pratt and Hommel 2003; Folk and Remington 2006; Adamo et al. 2008). This phenomenon was termed by Folk and colleagues (1992) as the contingent involuntary hypothesis and it states that:

"(…) involuntary orienting of attention to a stimulus event is contingent on whether that event shares a feature property that is critical to the performance of the target task" (Folk et al. 1992, p.1041).

In line with this evidence, superadditive attentional effects are present only when participant treat both modalities (visual and auditory) of the bimodal stimulus, as complementary (Calvert et al. 1999, 2000; Molholm et al. 2004; Johnson and Zatorre 2005). Furthermore, participants can resist stimulus-driven attention reorienting when they

are highly focused. It seems that abrupt onsets do not unavoidably capture attention, particularly when it is in violation of an observer's intention (Yantis and Jonides 1990). This is also seen in unimodal auditory attention, where "top-down control can trump involuntary attention switching to task-irrelevant distractor sounds (Sussman et al. 2003)" (Fritz et al. 2007b, p.187). Taking this evidence together, using a flash as an attentional control probe may contain too many disparate properties with the auditory target. Thus, is possible that attention was not (strongly) directed to the adapter. Furthermore, attending to the side of the adapter might be independent from attending to the adapter itself. Before the appearance of the probe, attention could have been devoted to the visual modality and could have been scattered across the two hemifields, since there is enough evidence showing that observers are able to attend to several simultaneous regions in space (as many as four non-adjacent locations; Kramer and Hahn 1995; Awh and Pashler 2000; Müller et al. 2003; McMains and Somers 2004). After the probe response, attention could have been reoriented to the adapter, but it was not possible to determine whether this was the case, thus, despite the attention probe being successful in tracking the attention allocation, it may have done so for the visual modality only, which could explain why attentional modulations were not observed in the auditory adapter.

The question that chapter seven proposed to answer was limited by several methodological constraints, most of them related to the behavioural nature of the experiment. Because adaptation is stronger when the adapting stimulus and probe are the same (i.e. adaptation is stimulus-specific; Briley and Krumbholz 2013), the same stimulus should be used to maximise the effects of adaptation. However, this

created difficulties in the control for attention deployments, as seen in the first experiment of this chapter. Conversely, although using a disparate attention probe (in our case, different modalities) might elevate the reliability of the attention control aspect of the experiment, this would come at an attentional cost for each object to be attended, in a manner of divided attention. For this reason, objective measures of neuronal behaviour (either by single cell physiology or uninvasive imaging) could be used to attempt to answer this question first, before proceeding to investigations of a behavioural psychophysical nature. Further experiments could, for example, adapt the paradigm developed in this thesis and combine EEG or fMRI recordings, while also integrating behavioural responses.

8.3. CONCLUSIONS

The ARE was first reported in the visual modality by Suzuki and Cavanagh (1997) but has since been a target of extensive research. For example, the ARE has been investigated under horizontal line bisections (Toba et al. 2011), colour manipulations (Gozli and Pratt (2012), luminance contours (Yamada et al. 2008) and even high-level motion (Shim and Cavanagh 2004). This rising number of ARE studies has created numerous research methodologies used to evoke the effect, which may have led to isolated reports. The difference in the findings of each study, particularly concerning the size of the repulsion, has made it harder to compare findings. For example, the bias observed in this thesis cannot be directly compared to other studies since it is a result of calculations involving the average between the bias recorded with the middle and either one of the side cues. Other studies often report the PSEs extrapolated for each side cue and take this as the measure of the size of the ARE (Suzuki and Cavanagh 1997; Arnott and Goodale 2006; Kosovicheva et al. 2010; Ono and Watanabe 2011). Furthermore, plenty ARE studies report the effect as observed by statistical testing (commonly ANOVAs) and express it as percentages of left/right responses without truly quantify the size of the perceptual shift (Pratt and Turk-Browne 2003; Pratt and Arnott 2008; DiGiacomo and Pratt 2012; Gozli and Pratt 2012; Au et al. 2013; Chow et al. 2014). For example, as stated in Chow et al (2014, p.5):"A significant effect of cue, $F(1, 15) = 55.88$, $p < .001$, $\eta_p^2 = .788$, $p_{rep} \approx 1$, revealed an ARE". Nevertheless, a positive outcome of this is that we now know of the existence of an established effect that has been observed in many different circumstances. Thus, the rising number of ARE studies created the need to standardise the methodology used to evoke this effect.

I have shown in this thesis that the ARE has the potential of bringing together different fields of science. For example, it can be argued that if attention is a supramodal phenomenon, then, using a visual or an auditory (or possibly a somatosensory) cue[40] will yield an ARE. It should not matter what is the modality of the attention-grabbing cue, if we consider attention to be supramodal. Moreover, having reviewed the field of divided attention, one could postulate that the ARE amplitude will be dependent on the attentional resources, and as such, cues from different modalities will add the cost of dividing resources across two different objects with different features to the size of the ARE: cues from the same modality as the target will yield bigger AREs, while cues from different modalities will generate smaller AREs.

The present thesis cannot satisfactorily clarify the neural substrates of the ARE since it is based on behavioural methods. On the one hand the ARE seems to receive contributions from attention deployments, but on the other hand, the current explanation for this effect (the position coding units hypothesis developed by Suzuki and Cavanagh, 1997) is in par with theories of adaptation, however, in this thesis, I could not disentangle the contributions of attention and adaptation to the ARE. Furthermore, this theory cannot explain the attraction effect when a cue is presented after the target, giving rise to the AAE. Also, it is unlikely that the units that code the position of the cues are the same or have overlapping receptive fields to those that code the central position of the targets. Agreeing with this notion was one of the results by the authors of the same theory: when varying the distance between cue and target, the authors did not find it to have any impact on the ARE. Thus, it can be argued that different units are coding the cues and the targets.

[40] that will automatically draw attention before presenting the targets

If the same units were involved in coding the position of both cues and target, then moving the cue farther from the target would decrease the ARE. Thus, either the ARE does not require the same units to be involved in coding both the position of the cues and the position of the targets (which would contradict the hypothesis formed by Suzuki and Cavanagh) or the ARE does indeed require the same units to code both cues and targets (in which case the results should show that increasing the distance between cue and target decreases the size of the ARE due to a lesser contribution of the units that code both target and cues).

8.4. FUTURE RESEARCH

In the previous conclusion section I argued how further research on the ARE could standardise the way the phenomenon is evoked, which would be the first step towards using the ARE as a tool to quantify the capture of attention. This has been suggested in the past by Pratt and Arnott (2008), since the ARE mimics results from RTs. If a further study is aimed at establishing a standard protocol that could inform the scientist on what is the best way to elicit the ARE, the following guidelines, which can be thought of a combination of features used in this thesis and previous studies, could make for a good starting point:

1 – dark backgrounds (where the visual stimuli is drawn) of 0.1 cd/m^2 or less;

2 – participant seating distances around 60 cm;

3 – dual-cue paradigms with central cue (upper-right and lower-left; upper and lower-middle; upper-left and lower-right).

4 – quantification of the ARE by computing a left-bias and right-bias measure with the middle cue as the central measure of perceptual bias, using the following formula: left cue – middle cue = left_bias; middle

cue – right cue = right bias; this way repulsion is a negative number and attraction a positive one.

5 – the ARE should be expressed in arcmin (1/60 degrees of arc) since the largest AREs are around one tenth of a degree.

6 – the temporal dynamics between cue and target are yet to be confidently determined but, ISIs as short as 16 ms and as large as 200 ms yield the best results;

7 – the spatial dynamics between cue and target are also an area of debate, but (on-screen) cue-target distances between 4° and 8° yield stronger effects;

More studies need to further characterise what cue type best elicit the phenomenon (squares, circles, triangles, high or low frequency sounds, etc), how the participant's distance to the screen impact the generation of the ARE, and further consolidate the temporal relationship between cue and target. Regarding the type of stimulus used, the luminosity also needs to be considered. To generate the ARE a wide range of luminosity values for the visual stimuli (cues, targets, fixation dot and masking squares) has been used in the literature. Studies have used 30 cd/m^2 (Pratt and Arnott 2008), 53.5 cd/m^2 (Suzuki and Cavanagh 1997), 69,40 cd/m^2 (Ono and Watanabe 2011) and 83 cd/m^2 (Kosovicheva et al. 2010), but since there is no convention on how to quantify the size of the ARE, it is hard to draw firm conclusions regarding the modulatory effect of the stimuli luminosity on this phenomenon. However, considering that brighter stimuli attracts more attention (e.g. Camgöz et al. 2004), one could predict that stimuli at 70 cd/m^2 would elicit a larger ARE than stimuli at 20 cd/m^2. Nevertheless, this is an area that needs to be explored and the following research question has not been addressed yet: At what brightness levels (high and low) does the ARE

operate? This would also impact the choice of cue, since filled circles will emit more light than open circles.

Regarding the relationship between the position of the viewer and the position of the cues and the targets, several avenues can be perused: one could inform about the impact that several viewer distances to the screen could have on the generation of the effect (also, would larger distances require bigger objects since spatial resolution has been decreased in favour of spatial coverage?); another avenue could inform about the way the phenomenon behaves when the cues are central and the targets[41] are displayed in the periphery; a further avenue could possibly study the phenomenon in different locations: the ARE has been studied in central perception, but, one could move the whole paradigm (fixation, cues and targets) to the left, right, upper or lower fields, and/or combinations of the fields (upper left, etc). This would define if the effect is restricted to the perception of the middle/centre, or if it changes according to foveated space.

Lastly, a more global phenomenon raised in this thesis concerns the effects of attention in sensory adaptation. The paradigm designed in this thesis was unable to answer this question, thus it is still open to debate what are the perceptual effects of attending to an adapter. Furthermore, since adaptation can been observed at all stages, from single neuron units to more complex neuronal structures (Lanting et al. 2013) and perception (Whitaker et al. 1997; but see Kohn 2007 for a review), and since (similarly) attention has been shown throughout this thesis to have influences in receptive field shifts and in perception, the implications of studying attentional influences in adaptation go beyond

[41] Because spatial resolution decreases towards the periphery of the visual field, new targets would have to be measured in order for the participants to discriminate between all of them

the perception of space, or even beyond the visual and auditory modality: the knowledge provided by such investigations will contribute to further expand our knowledge of the fundamental behaviour of single neurons and/or larger clustered structures. In conclusion it appears that the ARE is a phenomenon restricted to the visual modality, which is not surprising due to the better spatial properties of the visual system when compared with the auditory system, but the unimodal auditory ARE is yet to be measured confidently, thus if attention if the major contributor to the ARE, a smaller but present ARE could be possible in other modalities. Further studies on the ARE in other sensory modalities would probably be more successful investigating the somatosensory modality instead of the auditory modality, because the somatosensory system is also topographically organised, as is the visual system.

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Appendices

Appendix C.1 - Multisensory integration in the auditory cortex

This appendix will contain information regarding the work developed to study neural plasticity after sensory deprivation. This was the original intent of this thesis to which the student was awarded a joint scholarship of the School of Medicine and the Medical Research Council, UK. This appendix is structured in the classical IMRAD (introduction, materials, results and discussion) and will contain all the theoretical (literature review and aims) and practical work (electrophysiological experiments with live animal models) produced for the original research grant. After performing several in vivo experiments the original supervisors strongly advised me to discard the rest of the project due to their availability, but mainly because one other laboratory was involved in similar projects.

C.1.1 Introduction

One of the most important aspects of sensory experience is that it helps develop and differentiate neuronal structures. In the second section (Literature Review) I will cover what is presently known about the adaptations that take place in the cortex when there is no sensory input. I will discuss what factors induce these changes, how they are studied and how that reflects in our ability to live in a multisensory environment. More specifically I will review cochlear implantation studies, both human and animal, as they provide an exceptional opportunity for observation of plastic changes. I will attempt to gather recent developments of cross-modal changes in the auditory cortex and expose a gap in the literature where the present and other research studies are needed. One of the most significant current discussions in

neuroscience is the ability of a sensory cortex to welcome a change in its input modality. I will review how the sensory cortex may not be strictly mono-modal and has in reserve the ability to integrate multisensory stimuli, even in normal conditions of afferent input.

C.1.2 Literature Review

C.1.2.1 Loss of Sensory input

Research shows that the loss of auditory input is the trigger for physiological and functional changes that occur in the auditory system. We will see in this section how the auditory system is affected by deafness, firstly by briefly taking a look at the peripheral level, and later, by a more engaged review of higher cortical areas. Following this, we will see how the cortex of normal hearing participants is not unique in its function, but has an eclectic nature.

Auditory nerve changes with deafness:

Spoendlin (1975) studied different types and degrees of cochlear damage and observed that the retrograde degeneration of the cochlear nerve seems to be stereotyped to a sequence of histological changes. This sequence of events was described by Leake and Hradek in (1988), following the onset of deafness by ototoxicity in cats: "swelling, demyelination and degeneration of the peripheral dendrites; demyelination and shrinkage of the cell soma with preservation of the central axon; shrinkage of the ganglion cell and demyelination of the central axon; and loss of cell" (p.31). In both cases the neuron degeneration is incomplete, with few surviving peripheral dendrites. Most of this small population of cells corresponds to type II neurons, associated with outer hair cells, which are not involved in the transduction process. Type I neurons were greatly affected and the few

surviving cells show at least demyelinated of the distal parts of the central axon. It was observed that SGN degeneration continues for periods of at least four years following the drug insult to the cochlea (Leake and Hradek 1988).

Despite these and newer studies (Hardie and Shepherd 1999), the selective pattern of degeneration established in animals that seems to target type I neurons is challenged by Nadol's findings (1990) in human cases with long-term deafness. Nadol observed that the SGN cells in humans are morphologically different from those of other mammals and that despite the loss of the dendritic processes, the remaining ganglion cells persist for long periods of time (in one case, a sensorineural deaf ear had been deaf for thirty years). Furthermore, in humans, a survival advantage of type I neurons was observed in cochleae with reduced total SGN count where only 10% to 15% of the surviving neurons will be of type II (Nadol 1997). Since the SGN are the target for cochlear implants, this bears great importance for the success of the electric auditory stimulation. Literature suggests that the pattern and degree of SGN degeneration depends on a myriad of factors such as age at onset, aetiology, time spent in deafness and congenital and genetic causes (Leake and Hradek 1988; Nadol 1990; Xu et al. 1993; Leake et al. 1997; Hardie and Shepherd 1999).

Auditory cortex plasticity in deafness:

Although it is well know that subcortical nuclei can undergo changes in function (e.g. plasticity in MSO, Tirko and Ryugo 2012), studies show that the primary site for plasticity appears to be the cortex (Buonomano and Merzenich 1998). The remarkable ability of the cortex to undergo these changes is well documented in the literature and it is an increasing area of interest for neuroscientists. Research over the past 20

years has established that cortical maps, historically thought to be specific in function, are not constant, but dynamic. Plastic induced changes in the cortex are thought to be critical in some forms of perceptual learning, especially in cortical areas deprived of input. This is the case for CI patients, where the reintroduction of hearing via electrical means causes the auditory cortex to be re-joined with its old or 'purposely designed' form of perceptual stimuli.

As we will see, cortical adaptation is a function of time, with the more time spent in deafness working towards a greater take-over of the auditory cortex by other sensory modalities, leaving less neurons to be allocated for the processing of sound. In the presence of normal hearing input, the auditory cortex does not contribute to the processing of visual stimuli, but in the absence of hearing, the auditory cortex is responsible for an enhancement of visual performance (Lomber et al. 2010). The question whether this and other plastic changes that follow auditory deprivation are beneficial or detrimental to hearing with a CI is very much an open debate at the moment. On one hand, a visual take over means that more neurons can be allocated to the processing of visual cues and that visual-auditory interaction can be reinforced. This is particular importance since many cochlear implant users still rely on visual cues. On the other hand, the question remains whether the deaf auditory cortex will still represent the traditional acoustic cues when hearing is reinstated by a cochlear implant, or will remain engaged in visual processing as long as there is a visual input.

Animal research has documented several cases of plastic changes occurring following deprivation of auditory input. For instance, Allman and colleagues (2009) observed extensive conversion of the auditory cortex as a response to the loss of peripheral input. After 76 days of

deafness, 84% of the sampled neurons (in A1 and AAF) responded to somatosensory stimulation in the head, neck and face. This responsiveness was found in all layers of the cortical mantle and differed substantially from the hearing controls, where 96% of the sampled neurons in the same sites responded to auditory stimulation and none were activated by somatosensory or visual stimuli. Lomber et al (2010) compared the visual performance of congenitally deaf cats and normal hearing controls and observed that while peripheral localisation declined in hearing controls (between 60^{o}-90^{o} of the visual field), it was maintained at high levels of accuracy in deaf cats (performance significantly better for the 60^{o}, 75^{o} and 90^{o} positions). Moreover, movement detection thresholds were significantly lower in deaf cats. The enhancement in the visual localisation performance observed in deaf cats was attributed to the allocation of resources from deaf auditory cortex to visual processing. Simultaneous deactivation (via cooling loops) of primary and belt regions of the auditory cortex of deaf cats significantly reduced the visual localisation performance. This reduction was noticed solely in the most peripheral targets, where performances were earlier observed to be significantly better than hearing controls, and corresponded only to localisation skills and not detection. The authors also showed that visual functions that are not enhanced in deaf cortices (such as grating acuity, Vernier acuity, orientation discrimination, etc) do not redistribute to auditory regions, showing that there is not a complete reorganisation of visual processing maps, but rather a helping hand from the auditory cortex to increase the processing power of certain visual skills, but not all.

Studies with human patients were also able to observe that only certain aspects of visual attention are modified by deafness. In response to

colour changes there is no significant differences between normal hearing individuals and deaf individuals, whereas motion elicited event related potentials (ERP) of deaf individuals that were substantially enhanced when compared with hearing participants (Neville and Bavelier 2001). Moreover, Armstrong et al (2002) show that ERP responses are the same for NH and CI patients for colour stimuli, but not motion. Thus, animal enhanced visual abilities are in agreement with human studies: there is an enhancement of visual attention in deaf participants to peripheral moving stimuli (Neville and Bavelier 2001; Armstrong et al. 2002; Lomber et al. 2010)

Interestingly, plasticity is not an isolated phenomenon specific to the deprived sensory cortex. It is shared by other cortices that are not stripped of afferent input. In congenitally deaf mice, it was observed that after the take-over of the auditory cortex by visual and somatosensory responsive neurons, neurons in V1, that in normal controls responded vigorously to unimodal visual stimulation (97.92%), are now seen to respond to somatosensory (31.02% in NKCC1 mice and 1.07% in PMCA2 mice) visual (21.54% and 82.58%, respectively) and visual + somatosensory stimulation (47.44% and 16.35%, respectively, Hunt et al. 2006). Nevertheless, neurons in S1 remained predominantly unimodal in both mice strains, similar to normal hearing controls. Moreover, V1 in the congenitally deaf animals occupied a significantly larger area whereas the auditory cortex was significantly smaller than hearing controls. Deafness seems to shorten auditory cortical areas and enlarge other sensory areas (visual and somatosensory) that take-over the auditory space. There has also been an architectonic reorganisation between S1 and V1. The authors speculate that assignment of cortical

function during development could be a function of sensory experience. Experience also influences the size of the cortical fields.

It is an interesting question whether the functional organisation of the auditory cortex is preserved during periods of plastic changes. Initial research is encouraging. It has been shown that regions normally involved in localisation of acoustic stimuli contribute to the enhancement of visual localisation skills in the deaf cortex, thus maintaining its role in localisation, although now in visual rather than acoustic (Lomber et al. 2010; Meredith et al. 2011). Moreover, it seems the cortex is already prepared for cooperation between modalities. In normal hearing animals, inputs from visual areas into the auditory cortex were discovered and their function was suggested to be one of improving the spatial resolution of the auditory cortex (Bizley and King 2009) due to the greater ability of visual neurons to spatially encode sensory objects. This will be discussed in more detail in the next section.

C.1.2.2 Multisensory integration in normal hearing cortex

A recent study is able to show that visual stimulation alone elicits a larger activation of the auditory cortex in cochlear implant recipients than in normal hearing participants (Sandmann et al. 2012). In fact, a plethora of studies show activation of the auditory cortex in deaf individuals, but not in hearing individuals (Nishimura et al. 1999; Finney et al. 2001). However, Bavelier and Neville (2002) observed that despite the congenitally deaf individuals showing activation of the primary auditory cortex during visual stimulation, a small number of the hearing control also showed some activation of A1 when viewing alternations of moving and static dots. This alerted for the possibility that the cortex is multimodal in its nature, even in non-deprive individuals. Several Studies with human patients show multisensory

integration in healthy participants using EEG (Murray et al. 2005; Thorne et al. 2011; Cappe et al. 2012) or magnetic imaging (Bolognini et al. 2010; Gama and Lehmann 2015) techniques. However these studies are limited by non-invasive techniques and do not enjoy the spatial resolution that electrophysiological studies are capable. Despite this, human and animal studies have provided evidence for multisensory convergence in primary or belt regions of sensory cortices. Most dramatically, a series of experiments by Bizley and colleagues show a widespread of units sensitive to visual stimulation in primary and secondary regions of the auditory cortex (Bizley et al. 2005, 2007; Bizley and King 2009; Bajo et al. 2010). Importantly, these units were found to transmit more information when in response to bisensory (visual + auditory) stimulation than when one of these modalities alone. It is expected from a normal hearing cortex that the primary site is occupied by strongly auditory responsive units. This was confirmed by Bizley and colleagues (2007; 2009) where incidence of bimodal and vision specific cells was greater in higher order cortical areas than in core areas. In fact, the majority of visually responsive units were found in the anterior ventral field (AVF) which is thought to be the analogous region AES (anterior ectosylvian sulcus) in the cat (Ramsay and Meredith 2004; Manger et al. 2005). The cat AES contains multisensory neurons that represent the three modalities (somatosensory, visual and auditory) and thus is regarded as an association area (Wallace et al. 1993; Jiang et al. 1994). Nevertheless, since visual sensitive units were found in all cortical depths sampled, Bizley et al (2007; 2009) speculated that visual inputs to auditory cortex are not restricted to specific layers. The authors show evidence of projections from early visual areas to auditory cortex, which could underline the visual responses, found. However, Allman and colleagues (2009) observed vigorous responses to

auditory stimuli in normal hearing animals but none of the recording sites were activated by visual or somatosensory stimuli. The authors failed to identify significant cross-modal facilitations when the auditory stimulus was combined with visual (1 facilitation; 3 suppressions; out of 111 neurons) or somatosensory stimulus (2 facilitations; 2 suppressions; out of 111 neurons tested). These findings ruled out unmasking of pre-existing synapses as a candidate for the mechanism behind the cross-modal plasticity seen. In fact, within 16 days of deafness cross-modal reorganization of A1 was present but newly formed cortico-cortical connections were not found by Allman and colleagues. As a result, the authors question if the reason for this strong take-over of the auditory cortex might be a consequence of changes that occurred or instance in distant sub-cortical locus in the brainstem (Allman et al. 2009). Despite these findings, auditory, multisensory and visual neurons coexist in the adapted auditory cortex of lesioned ferrets, suggesting that a cooperation between modalities, instead of a competition of one input over the other, could be possible (Mao et al. 2011).

C.1.2.3 Cochlear implantation and cortical plasticity

How a cochlear implant works:

The cochlear implant (CI) is arguably the most successful neural prosthesis to date. It started out as a single electrode device that mainly provided sound alertness without contributing much to aural communication, evolving to aid in lip reading and enhancing speech perception. The CI can restore auditory function to sensorineurally deaf ears through the direct electrical stimulation of the SGN cells with electrical pulses bypassing the IHC (the transducer mechanism) located in the Organ of Corti. This chapter briefly describes the cochlear

implant and how it works. See Loizou (1998), McDermott (2004), Zeng (2004) or Clark (2006) for a more complete review of its operational aspects.

Today, the CI is a highly developed multielectrode device that aids a vast range of individuals. Children as young as 3 months and adults with substantial residual hearing (at lower frequencies) can now also enjoy the benefits of this technology. The primary components of a cochlear implant are depicted in figure1. All the current systems share universal components that include internal and external parts. The internal parts are surgically implanted into the mastoid bone and comprise an electrode array (that is inserted into the scala tympani through the round window), and a receiver/stimulator (that is placed either in a bone pocket or tucked away between the mastoid and the scalp). The external worn parts include a microphone (either condenser/electret or piezoelectric), a BTE speech processor, and a circular aerial.

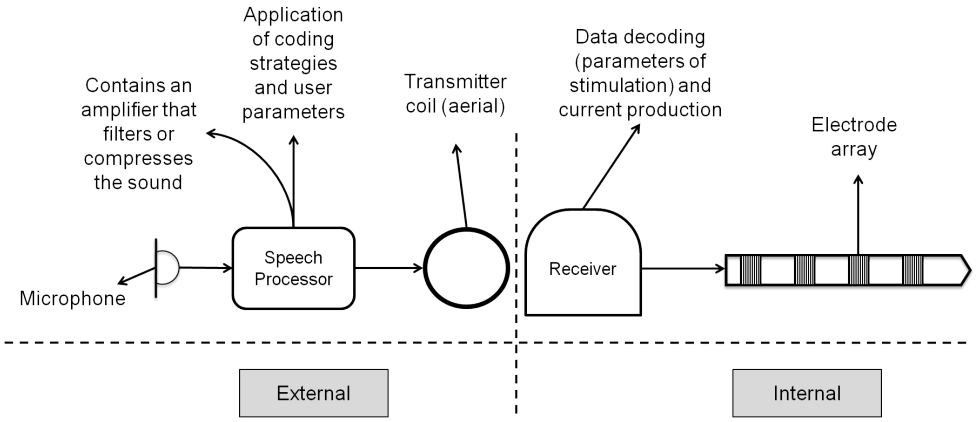


Figure A-8-1 – Basic components of a current cochlear implant system (adapted from McDermott, [2004])

The acoustical energy from a sound source reaches the microphone (often with a directional polar pattern) and is converted into electrical energy before serving as input to the speech processor. Here, the signal from the microphone is divided into the different frequency bands,

user-specific parameters are encoded and the resulted code is transmitted to the surgically implanted parts via the circular aerial. The external aerial and the internal receiver are held together by a magnet and form a transcutaneous inductive link that delivers the digital code from the speech processor. This link also supplies the implanted electronic parts with electric power; this communication is done using radio frequencies (McDermott 2004). The internal receiver decodes the signal transmitted by the speech processor, which stipulates the temporal parameters, the amplitude and the particular electrodes that are to deliver the current, in the form of biphasic current pulses. The electrode array will be introduced into the cochlea in an effort to replicate its tonotopicity: low frequency sound will be allocated to the deeper electrodes and high frequency to more basal electrodes. While many current cochlear implants can have specific components and different designs, the operational principles remain the same.

Critical period for brain development

Our sensory cortex is capable of extensive plasticity following deprivation or damage of afferent pathways. This reorganisation is especially strong when the insult occurs at early stages of development, with the subsequent functional maturity of the cortex crucially dependent on sensory experience (Kral et al. 2005). In 2004 the population of cochlear implant users surpassed the 60 000 recipients (McDermott 2004). Today, there are more than 200 000 cochlear implant users worldwide (Kral and Sharma 2012), 80 000 of which are children (Kral and O'Donoghue 2010). The age of implantation has taken an important role in performance with a CI, thus studies of a critical period for brain development have shed some light on how functional changes in the cortex due to deprivation are affected by age. This developmental

window showed a stronger plasticity. After this period the effects of chronic stimulation on the auditory system were found to decrease. Cats implanted after this sensitive period showed worse activation of the auditory cortex when compared with cats implanted earlier (Kral et al. 2002) even with longer periods of cochlear implant stimulation. This seems to suggest that age at implantation plays a stronger influence to implant performance than experience with a cochlear implant. This is confirmed by human studies. P1 latencies of the CAEP have been extensively used in normal hearing and hearing impaired children as a biomarker for cortical development of the central auditory pathways (Sharma et al. 2005b; Dorman et al. 2007; Kral and O'Donoghue 2010). This tool allowed several studies to identify a cut-off age for optimal auditory cortical plasticity. Implantation during this period is shown to yield the best results. Sharma et al (2002) observed that 96.5% of the early implanted children (implanted by age of 3.5 yr; average age of implantation of 2.3 yr) had P1 latencies that fall within the range of age-matched normal-hearing children, with later times of implantation having progressively worse scores (65.5% of the middle-implanted [average age of implantation of 5 yr] and 95.2% of the late-implanted [average age of implantations of 11.2 yr] groups falling outside the normal range). This effect was observed despite the fact that all participants were not significantly different with respect to duration of implant use. In summary, animal and human studies are in accordance regarding the existence of a critical period for plasticity and boy show that age at implantation plays a more critical role than experience with a CI. In a longitudinal study, Sharma et al (2005a) compared two groups of children in the age cut-offs defined earlier as early-implanted (<3.5 yr) and late-implanted (>7 yr) and observed that both P1 latency and wave morphology were significantly different between the groups.

Late-implanted children showed atypical latencies and waveform morphology during the first year of implantation while the early-implanted group showed a rapid development (within the first week P1 latencies resemble those of normal-hearing newborns). Despite the important role of age at implantation, we know that experience with a cochlear implant also induces functional changes in the auditory system (Sandmann et al. 2009) and that rehabilitation cannot be undervalued.

Plasticity in CI users (benefit and detriments)

In quiet or easy listening conditions one might not be aware of the importance of visual cues for speech recognition but this becomes increasingly significant during speech in noise. Helfer and Freyman (2005) showed in normal hearing participants that visual cues provided greater benefit for both recognition and detection of speech, where a competing masker (steady-state noise or competing voices) was presented coincidentally or from different spatial locations with the target speech. In cases of profound deafness, speech reading abilities become crucial to communicate. Normal hearing listeners have poor speech reading abilities (Summerfield 1992) that worsen with age (Sommers et al. 2005), but profound deaf participants are able to transport their speech reading abilities acquired during the period of deafness to hearing with a CI. These patients maintain a higher level of word recognition in speech reading conditions when compared with NH controls (Rouger et al. 2007). This effect seems to persist even for years after implantation. When the authors compared the audio-visual performance of CI users and NH listeners (exposed to degraded auditory stimuli) they again observed higher gains in CI users suggesting that the multisensory integration that was acquired during deafness remains after implantation. Thus, implantation may enhance

cross-modal changes as a specific compensatory strategy to cope with the degraded auditory signal. In fact, research shows that lip reading abilities and speech understanding improve with cochlear implant experience, showing evident gains in the first years of implantation (Tyler et al. 1997; Giraud et al. 2001). Moreover, functional neuroimaging experiments show that CI users recruit the visual cortex when listening to words (Giraud et al. 2000), an effect that was significantly weaker in normal hearing controls. This activation increases with implant use and it appears to be stimulus specific. In particular, visual cortex activations were observed for meaningful sounds such as words, syllable strings and environmental sounds, but not for meaningless noises(Giraud et al. 2000, 2001). This suggests that the cross-modal reorganisation acquired in deafness gets readjusted further to represent specific sound categories (Giraud et al. 2001). The authors found a strong positive correlation between lip reading abilities and the strength of the activation of the visual cortex to both words and syllables. This supports the notion that CI recipients use the necessary visual cues to disambiguate words and syllables, and that in this case, the plastic changes that occur in the auditory and visual cortices are beneficial. Other studies were also successful in correlating responses to visual stimulation and speech recognition abilities. Cochlear implant users with good speech perception showed enhanced brain activation in response to visual stimuli that is confined to the visual cortex, while in contrast, poor cochlear implant performers show additional cortical recruitment (anteriorly to V1) to process visual stimuli (Doucet et al. 2006). This relationship could reflect a better use of visual cues by good CI users to compensate for the degraded CI signal.

Despite this, it has been suggested that cross-modal reorganisation of the AC, limits the benefit from a CI. It seems that once the auditory cortex in prelingually deaf participants exhibits an extensive cross-modal reorganization, it can no longer respond accurately to signals from a cochlear implant (Lee et al. 2001, 2007; Giraud and Lee 2007). In fact, there is an increased neural activity of the auditory cortex during period of deafness (manifested by increase blood flow and increased glucose metabolism). If there is no auditory input to the cortex, we can assume this activity comes from other sensory regions in the brain. Not surprisingly, this activation has been shown to be negatively related to speech perception abilities after implantation (Lee et al. 2001). As duration of deafness increases so does the metabolic activity of the deaf cortex, leading to poorer speech scores and smaller activation of the auditory cortex when later reunited with hearing sensations via a CI. There are in reality a number of studies that show a maladaptive reorganisation of the auditory cortex, where poorer speech scores after implantation are associated with time spent in deafness (Waltzman et al. 2002; Gomaa et al. 2003; Kelly et al. 2005; Doucet et al. 2006). *De facto*, duration of deafness is the most negative influence on performance with a CI out of aetiology and age at implantation (Blamey et al. 1996). Perhaps time allows for plastic changes to become more definite and harder to reverse if the competing input remains active. It seems the duration of deafness allows compensatory changes to take place in the auditory cortex, with larger periods allowing for more areas of the auditory cortex to be activated in response to visual stimuli (Doucet et al. 2006).

One way or the other, electrical stimulation is thought to improve the auditory pathways at peripheral and central levels. Animal studies

show that electrical stimulation helps preserve SGN (that would continue to degenerate in deafness) in cats (Shepherd et al. 1983, 1994; Leake et al. 1991), and guinea pigs (Losteau 1987; Li et al. 1999), and that in some cases it induces augmentation of cell size (Leake et al. 1999). Electrical stimulation of the auditory nerve resulted in an increase in size of axodendritic boutons, where despite of being smaller than normal hearing controls, they were significantly bigger than deaf participants (Tirko and Ryugo 2012). Moreover, electrical stimulation changed the synaptic organization of the medial superior olive, which had now inputs that appeared statistically similar to normal hearing controls. Thus, electrical stimulation through a cochlear implant is also responsible for plastic changes at synapse level. The restoration of auditory input leads to morphological and organisational changes of principal cells of the medial superior olive (Tirko and Ryugo 2012).

Human studies report a functional improvement in cortical auditory centres. Activation of both primary and belt regions of the auditory cortex was observed in CI patients, one week after implant switch-on in response to noise and speech. At this point this correlated with the inability of these recipients distinguish between noise and speech (Gama and Lehmann 2015), but after this period, the authors consistently observed a reduction in the number of activated clusters in the secondary regions and a better tuning of the primary auditory region. This supports the notion that during deafness the AC loses its specificity, becoming fine-tuned with implant use. Exposure to electrical stimulation leads to auditory cortical regions to be gradually recruited to represent the auditory stimulus. It has also been shown that the degree of this recruitment is correlated with experience with a CI, in

early implanted participants, but the effect is smaller in late-implanted participants (Kral et al. 2002).

To finalise, Cochlear implant studies also show that users undergo changes that are not restricted to the deprived auditory cortex. In fact, long-term deprivation of auditory input leads to functional changes in the central visual system (Bavelier et al. 2006; Mitchell and Maslin 2007). When compared with normal-hearing listeners Bavelier et al (2001) show increased activation of visual cortex to motion stimuli in the peripheral visual space while Armstrong et al (2002) showed increased VEP amplitude produced by deaf participants. These studies show greater recruitment of the visual cortex in deaf than hearing adults.

C.1.2.4 Aims

Presently, it is accepted that higher cortical sensory areas are not populated exclusively by modality specific neurons: multimodal interactions (auditory/visual) occur in core and belt regions of the auditory cortex of hearing animals. In particular, visual specific and bi-sensory (visual/auditory) neurons were found in the auditory cortex of ferrets (Bizley et al. 2007). Despite these findings, Allman et al (2009) reported that the vast majority of cortical auditory neurons tested (in the same animal) did not reveal any significant non-auditory influences and that the average responses to auditory, auditory+visual and auditory+somatosensory stimuli did not differ significantly. Furthermore, the neurons in deafened animals that project to A1 had their projections originating in the same area as hearing animals and no connections were found between the auditory cortex and the somatosensory ventrobasal complex. In contrast, Bizley et al (2007) found strong inputs to MEG and PEG arriving predominantly from

areas 20a and 20b (visual form). Therefore, our initial experiments seek to establish the prevalence of multisensory responses in the auditory cortex of normal hearing ferrets. Following this we proposed to study how these responses are affected by deafening, and finally, to investigate the effect of reintroduction of hearing with a cochlear implant on any cross-modal plasticity that we hypothesised to observe in deafened animals. We initially conducted a series of pilot experiments with ferrets, which seek to establish a suitable animal model for the above-mentioned purpose. These initial experiments are detailed next.

C.1.3 Methods

C.1.3.1 Animal preparation

Anaesthesia was induced by an intramuscular injection of medetomidine hydrochloride (Domitor, 0.08 mg/kg; Pfizer) and ketamine (Ketaset 0.08 ml/kg; Fort Dodge Animal Health). At the time of induction, an intramuscular injection of atropine sulfate (0.06 mg/kg; C-Vet Veterinary Products) was given to reduce the risk of cardiac arrhythmias and to limit airway secretions. After induction, a 24-gauge cannula was inserted into the cephalic vein and anesthesia was maintained with a continuous drip of a mixture of medetomidine hydrochloride (0.02 mg/kg /h) and ketamine (Ketaset, 5 mg/kg/h; Fort Dodge Animal Health) in a 5% glucose-saline solution, diluted in a 50 ml syringe. The animal was intubated with a 3-mm internal diameter, uncuffed, endotracheal tube (ET; Portex, Smiths Medical International) inserted under direct laryngoscopy (the ET tube was subsequently stitched to the animal's cheeks to prevent being displaced by potential sudden spasms of the airways). The animal was placed in a warm blanket and ventilated with an oxygen-air mix (rate 39 strokes min^{-1};

stroke volume 3.5 ml). Its body temperature (via rectal thermometer), end-tidal CO2 , and electrocardiogram were monitored throughout the experiment. The right and left eyelids were stitched open and protected with liquid paraffin solution (Lacri-Lube; Allergan inc). The animal was placed in a stereotaxic frame, and the right and left pinnas were removed to expose the external auditory meatus, where the speaker speculae were inserted. The temporal muscle was removed to expose the dorsal and lateral parts of the skull and a stainless steel bar was attached to the frontal region with stainless steel screws and dental cement, eliminating the need for the stereotaxic frame.

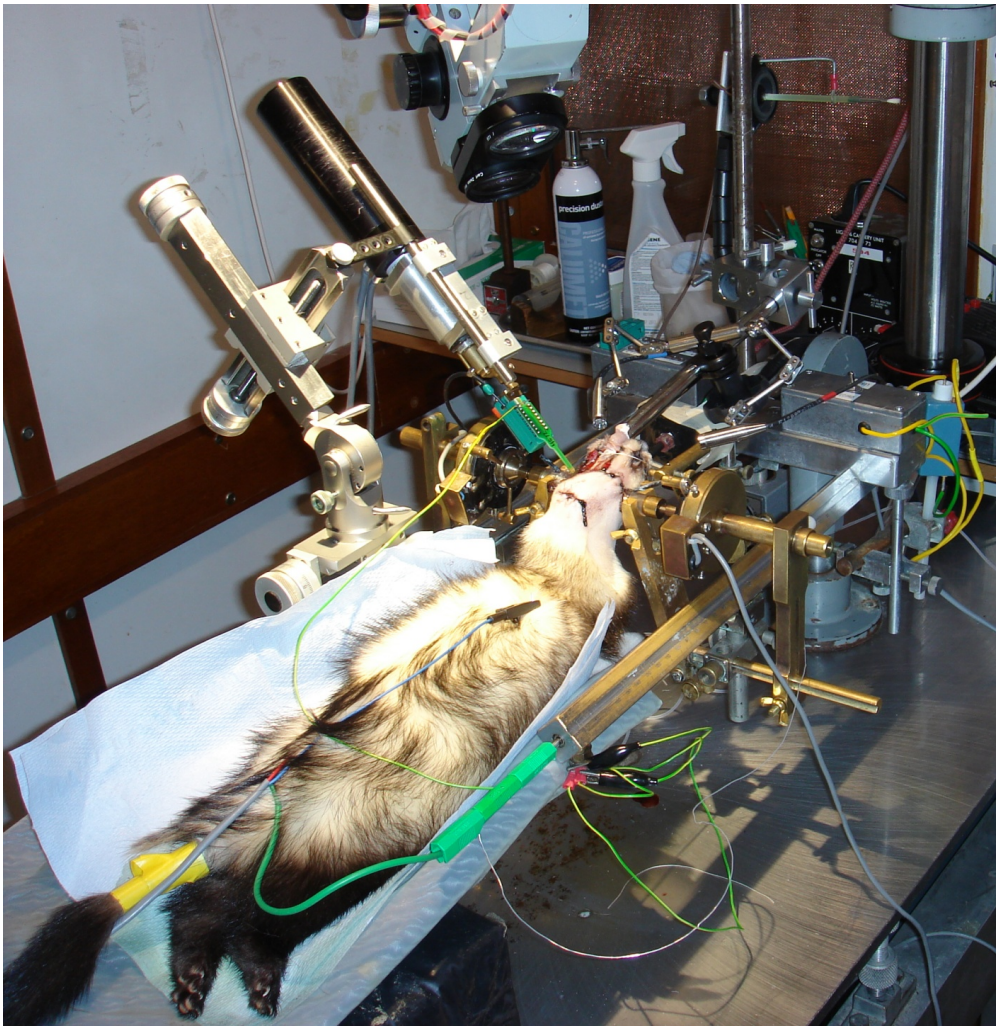


Figure A-2 Anaesthetised animal in stereotaxic frame.

A craniotomy was made over the left middle ectosylvian gyrus (MEG) to expose the primary auditory cortex (A1; 11 mm from Nuchal Crest and 7 mm from Sagital crest). The dura layer was removed and a 1.5% agar solution applied to protect the cortical surface and improve recording stability. The visual stimulating apparatus, consisting of two LEDs mounted in robotic arms, was placed in front each eye and the electrophysiological recordings were carried out. Figure A-2 shows the prepared animal under sedation.

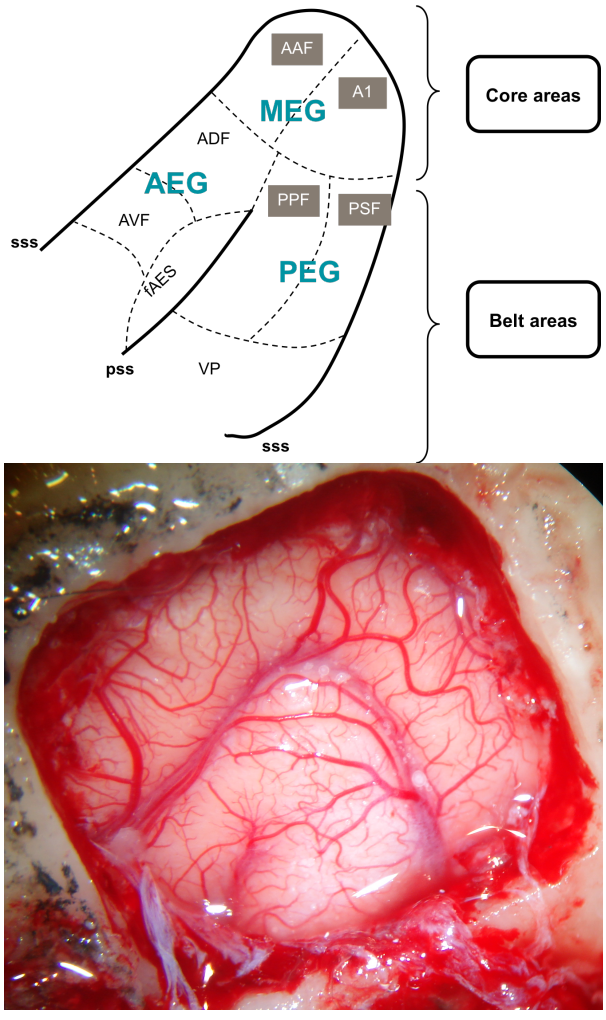


Figure A-3 Lateral view of the ferret left auditory cortex located in the ectosylvian gyrus (EG) and bounded by the suprasylvian sulcus (sss). Primary areas are located in the medial ectosylvian gyrus (MEG) and comprise the anterior auditory field (AAF) and the primary auditory cortex (A1). PEG – posterior ectosylvian gyrus; PSF – posterior suprasylvian field; PPF – posterior pseudosylvian field; VP – ventral posterior; AEG – anterior ectosylvian gyrus; ADF – anterior dorsal field; AVF – anterior ventral field; fAES – anterior ectosylvian sulcal field; pss – pseudosylvian sulcus. Regions highlighted in grey are tonotopically organised.

Figure A-3 shows a close-up photograph of a representative auditory cortex after craniotomy and before the agar protective layer. These procedures were licensed by the UK Home Office.

C.1.3.2 Neural recording

To find out if the units were acoustically responsive a diotic broadband noise (110-dB SPL; 0.05- to 50-kHz bandwidth; 100 ms duration with a 2 ms cosine-squared rise-fall time) was used. The visual stimulus was a diffuse light flash, which did not vary in intensity, presented from two light-emitting diodes that were usually fixed at a distance of 10 cm from both eyes so that it illuminated virtually the whole of the visual field. Acoustic search stimulus and light flashes were presented simultaneously as a search stimulus in order to find any responsive units.

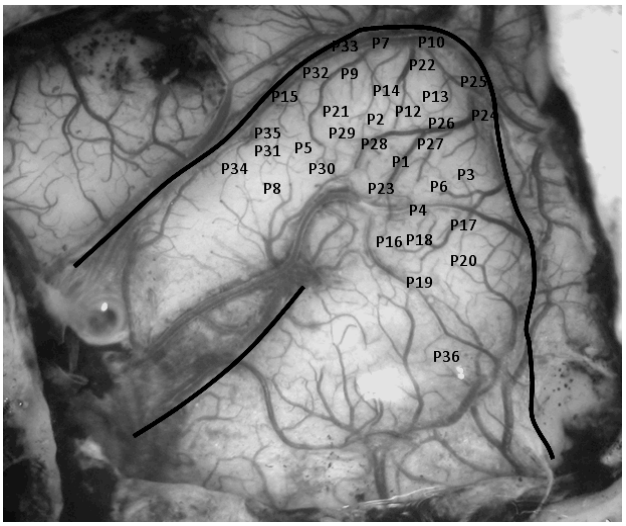


Figure A-4 representative left auditory cortex. Number are penetrations sites made at different depths superimposed in a photography of the auditory cortex of a normal hearing ferret. Recordings were primarily made in the medial ectosylvian gyrus (MEG: A1 + AAF) and boundary areas with the posterior ectosylvian gyrus (EG: PPF + PSF; shaded areas). P1 is penetration 1.

Once neuronal activity was found to be driven by the search stimulus, frequency response areas were performed to establish the centre frequency of the cell or clusters of cells. The frequency tuning of each

responsive unit was characterised with pure tones (100ms duration with a 2 ms rise-fall time) over a range of frequencies (58 Hz to 21 kHz in a one octave step) and levels (95-5 dB SPL in 5 dB steps) and centre frequency (CF) was defined as the tone frequency that elicited the largest number of spikes in a 500ms window after stimulus onset. Each presentation had a stimulus length of 100ms, a sweep length of 500ms and a repeat rate of 800ms. The CF was used to subsequently determine whether the cell was preferentially acoustic, visual or bisensory by presenting the CF stimuli and light flashes simultaneously or individually. After the light and sound condition had been recorded, reaction to somatosensory stimulation was investigated using a fine paintbrush and manually searching in the cheek, face, neck and body for any driven activity. The somatosensory apparatus consisted of paintbrush hairs glued to a speaker cone (controlled via Brainware) and was put in place in case any driven activity had been found in the manual search. All stimuli were generated with Tucker-Davis Technologies System III hardware, Brainware and Real Time Processor Visual Design Studio (RPvdsEx) software (50-kHz sampling rate). Prior to the experiments closed-field calibrations were performed using an 0.5 inch condenser microphone (Brüel & Kjaer, UK).

C.1.3.3 Subjects

Ten adult (with age ranging from 2.5 to 5.5 years) normal hearing pigmented Ferrets (Mustela Putorius; average weight 1316.7 Kg) were used in this study. Three animals died during the surgery, before data was collected, and a further 2 animals did not present any driven responses.

C.1.4 Data Analysis and results

The data analysis performed encompassed two steps: a spike sorting step and a descriptive statistical step. An automatic k-means clustering algorithm from BrainWare was used to perform the offline sorting of spikes. An autocorrelation was used to separate clusters from single units, with the later being defined as having a clear refractory period in the autocorrelation histogram. Figure A-5 illustrates an example of spike sorting from a single electrode.

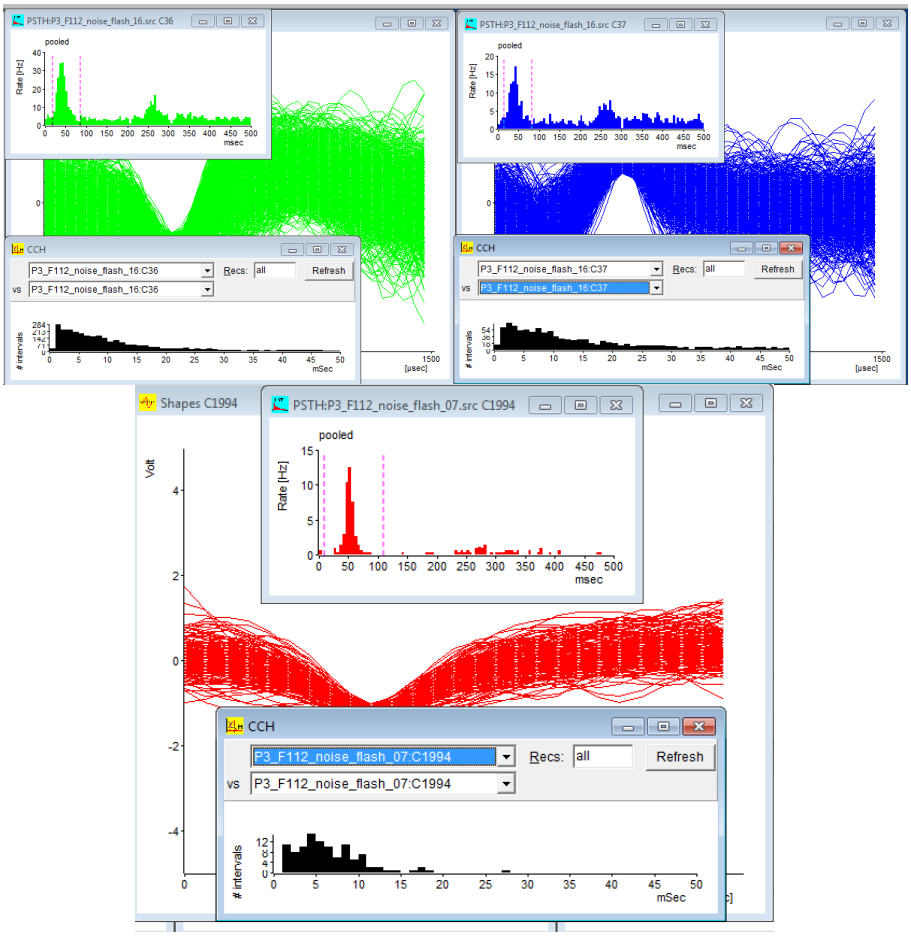


Figure A-5 On top, example of spike sorting from one electrode. This electrode picked two different clusters (green and blue). On the bottom, an example of a single unit and its autocorrelogram.

After applying the k-means algorithm, an autocorrelation was performed in the three observed spikes. The graph in red represents a single unit while the green and blue graphs are two different clusters.

Neuronal activity was found in 43% of the penetrations (22 in 51). Out of these "good" penetrations, only 39% responded to our stimulus, with 61% of the recordings being unresponsive. Further descriptive analysis revealed that 92% of the action potentials (AP) recorded were driven by sound alone (127 of the 138 sampled neurons), 7% were bisensory units, responding to sound and visual stimulation (of these, 30% showed a facilitation when auditory was combined with visual stimuli; an example of this is the bisensory cell depicted in figure A-6); the remaining evoked responses (1%) were from cells that were only driven by the light. In the primary areas of the auditory cortex 8% of the sampled neurons responded to a form of visual stimulation, either alone or in combination with sound. Thus far, we have failed to reveal any somatosensory influences in primary areas of the Ferret's auditory cortex. Depicted below are examples of the four cell types found.

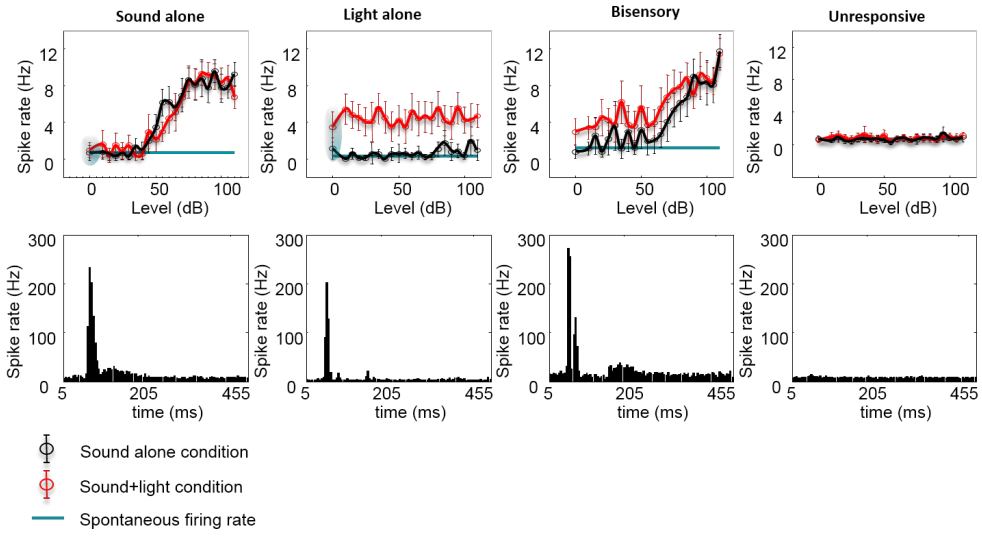


Figure A-6 example of cells with different sensory response types. From left to right: auditory cell; visual cell; bisensory cell (with facilitation when both stimuli are combined); unresponsive unit; Error bars are SD

In the sound alone cell, the activity driven by the sound was not different from the activity driven by the light. The unimodal visual cell in the second column responds to the light only, and the responses to sound do not appear to be significantly different from the stochastic

firing rate. The bisensory cell is driven by sound, depicted by the black line, and the firing rate increases when sound is combined with light, until both lines intercept at around 90dB SPL (which shows saturation of the cell). This cell responds to light alone, given by the red line condition (sound + light), at the 0 dB SPL condition. In other words, looking at the 0 dB SPL of the red line, indicates the visual alone condition (since attenuation of sound is maximum at this point).

The activities of the two conditions (sound alone and sound+light) were not compared further, thus no conclusions can be drawn regarding the statistical differences. This means that (although error bars show standard deviations) we cannot conclude that the driven activity of one condition is significantly different than the other condition for a given cell. The above remarks are observations of the graphical outputs.

Appendix C.3 – Appendix of chapter 3

Psychometric functions:

```
%{
Extended Sigmoid:
((1-0.5-l)./(1+exp(-(x-alpha)/beta)))*100
============
Logistic:
(1./(1+exp(-1*(beta).*(x-alpha))));
============
Cumulative:
(1+erf((x-alpha)/(sqrt(2)*beta)))/2;
============
Gumbel:
(1-exp(-1.*10.^(beta.*(x-alpha))));
============
Weibull (the Weibull function is not defined for negative stimulus intensity values.)
(1 - exp(-1*(x./alpha).^beta));
%}
```

Appendix C.5 – Appendix of chapter 5

Middle cue t-test. Output from SPSS

One-Sample Test						
	Test Value = 0					
	t	df	Sig. (2-tailed)	Mean Diff	95% Confidence Interval of the Difference	
					Lower	Upper
Mcue16	-.816	29	.421	-.01194	-.0419	.0180
Mcue50	-1.444	29	.159	-.02306	-.0557	.0096
Mcue100	-.921	29	.365	-.01681	-.0541	.0205
Mcue167	-.288	29	.776	-.00577	-.0468	.0353
Mcue200	-.039	29	.969	-.00056	-.0297	.0285
Mcue500	-1.437	29	.161	-.02419	-.0586	.0102

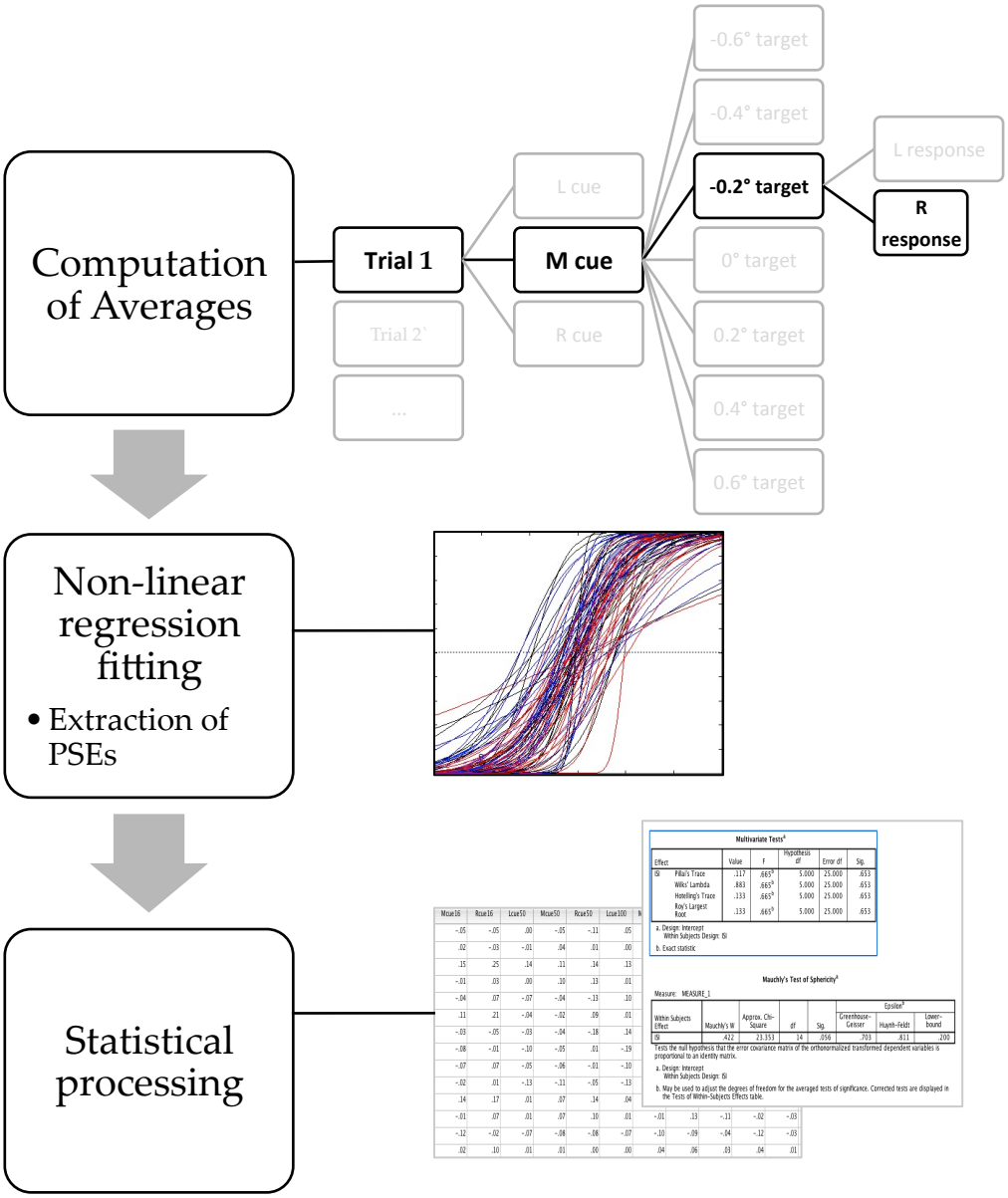
Appendix C.6 – Appendices of chapter 6

C.6.1 - Exclusion/inclusion of participants in the AA ARE.

Exclusion/inclusion of participants per ISI. Crosses represent exclusion due to poor NLRM estimation. Green are selected participants, yellow are those participant that were excluded in one ISI only.

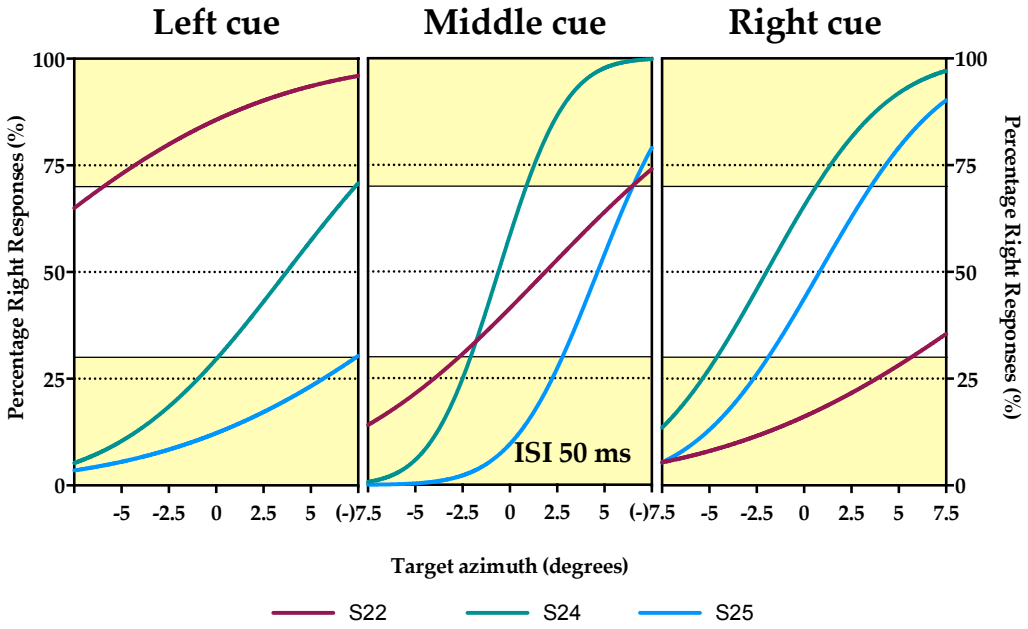
	16 ms	50 ms	100 ms	167 ms	200 ms	500 ms
S1			✖	✖	✖	
S2					✖	
S3	✖	✖	✖	✖	✖	
S4	✖	✖	✖	✖	✖	✖
S5	✖	✖	✖		✖	
S6		✖	✖		✖	✖
S7						
S8	✖					
S9						
S10				✖		✖
S11	✖	✖	✖	✖	✖	
S12						
S13					✖	
S14			✖	✖	✖	
S15						
S16						
S17			✖	✖	✖	
S18	✖			✖		
S19	✖	✖	✖		✖	
S20		✖				
S21	✖	✖			✖	✖
S22		✖				
S23					✖	
S24		✖				
S25		✖				
S26	✖		✖		✖	
S27	✖	✖	✖	✖	✖	
S28						
S29					✖	
S30						
S31	✖					

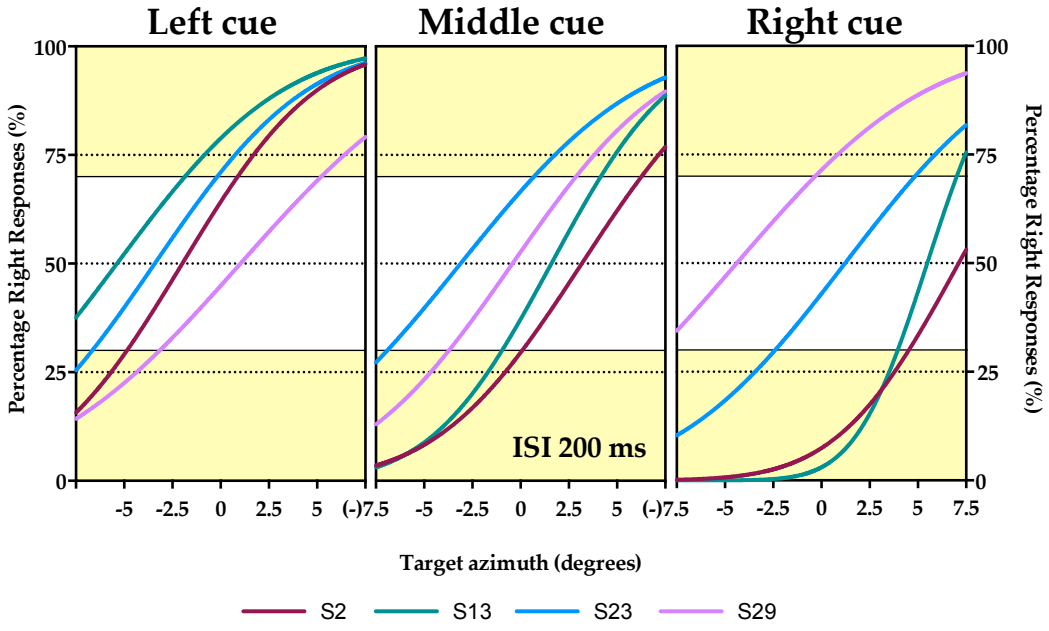
C.6.2 – Data Analysis pipeline



C.6.3 - Analysis of excluded participants

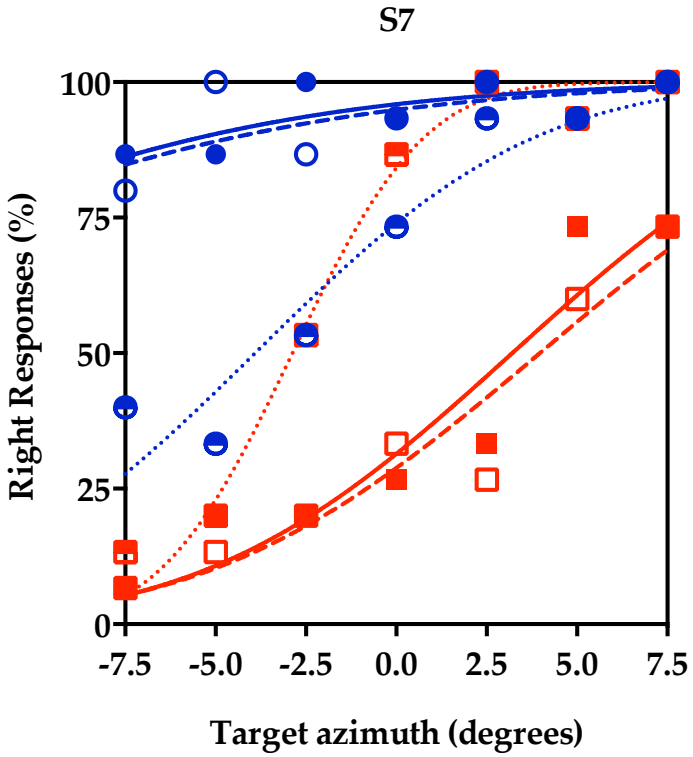
Graphics of excluded participants. These are the yellow rows of appendix 1, the participants that were excluded in one ISI only and were reanalysed after the performance threshold (third exclusion criteria) was relaxed to 70%. ISI 50 ms on top and 200 ms on bottom.

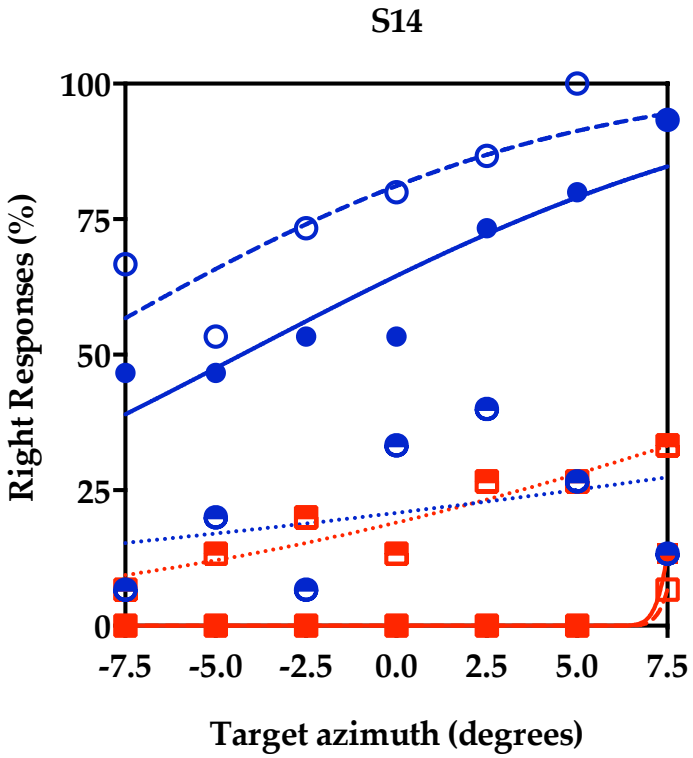




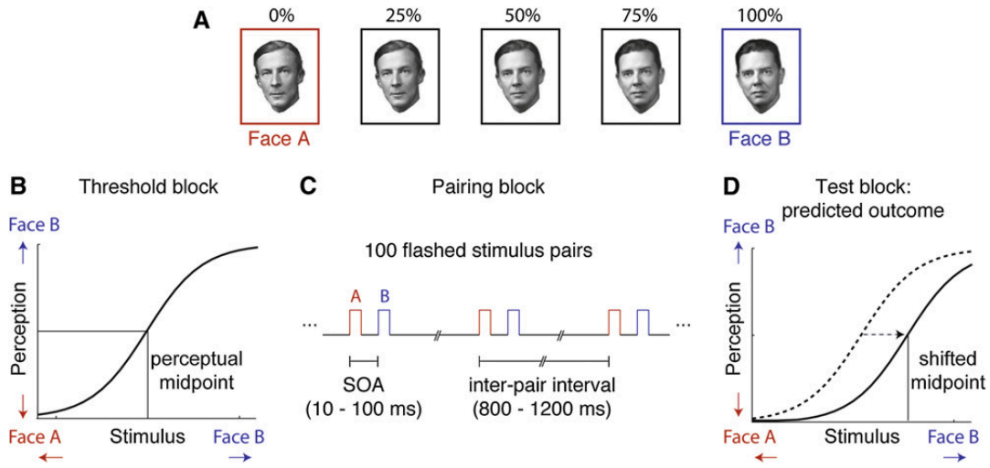
Appendix C.7 – Appendices of chapter seven

C.7.1 – Excluded participants of experiment 7





C.7.2 - An example of behavioural STDP from McMahon and Leopold (2012)



Depicted here is figure 1 of McMahon and Leopold 2012 showing the stimuli used to induce perceptual shifts for face identity (A: two faces were used as stimulus A and B, with three morphed faces in 25 % contribution steps). Figure B represents the threshold block, using the MCS, to determine the morph level that was equally likely to be perceived as face A or face B. Figure C represents the pairing block (either A-B or B-A), and figure C represents the predicted test block, where the participant's perceptual midpoint was shifted. Copyright permission from CCC, license 3870820030553

C.7.3 - Figure from Briley et al (2013)

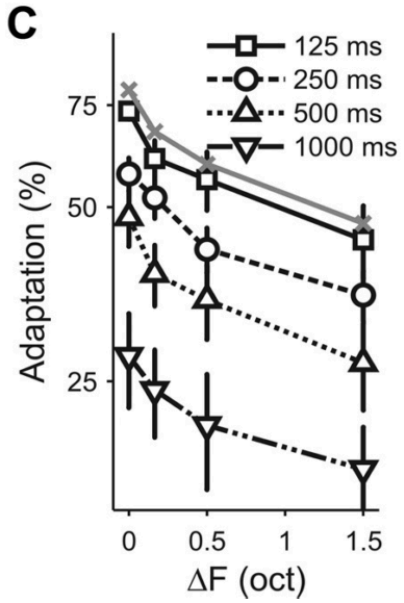


Figure 1C (with permission) of Briley et al (2013) showing the relationship between percent adaptation and the frequency separation between adapter and probe (Δf). Each symbol corresponds to one adapter-probe SOA. The grey line is the extrapolated SOA of 0 ms. Adaptation was measured as a relationship between the adapted probe responses and unadapted probe responses, expressed as a percentage. The adapter and probe were both pure tones of 110 ms duration presented during 5s. The authors also varied the adapter-probe SOA and adaptation was shown to decrease and a function of this temporal distance.

C.7.4 - Individual visual thresholds

Table 5 Threshold of attention probe as measured three times by a luminance meter.

Subject	Matlab level	Reading 1 (cd/m^2)	Reading 2 (cd/m^2)	Reading 3 (cd/m^2)
1	23.95	0.47	0.47	0.48
2	30	0.69	0.77	0.75
3	36.87	1.30	1.23	1.23
4	20.20	0.24	0.30	0,.33
5	33.96	0.98	1.04	1.07
6	24.58	0.48	0.48	0.49
7	22.50	0.39	0.39	0.41
8	26.25	0.54	0.55	0.57
9	23.12	0.43	0.42	0.43
10	44.16	1.80	1.81	1.84
11	22.50	0.41	0.41	0.41
12	24.37	0.45	0.48	0.49
13	45.41	2.01	1.98	1.98
14	36.23	1.10	1.15	1.15
15	23.54	0.43	0.43	0.48